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THE JOURNAL OF AGRICULTURAL SCIENCE

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AND THE ROTHAMSTED RESEARCH INSTITUTES BY

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SOIL IMPROVEMENT IN THE SUDAN GEZIRA

By H. GREENE AND O. W. SNOW

Agricultural Research Service, Sudan

(With Four Text-figures)

INTRODUCTION

ABOUT 1000 square miles of the Eastern Gezira are irrigated from the Sennar Dam. The soil (Joseph & Martin, 1923; Joseph, 1925; Joseph & Whitfeild, 1927; Greene, 1928) is a heavy clay, strongly alkaline, of low permeability to water, and low in content of nitrogen and humus. Sulphates of sodium and calcium are present in the soil, and although the irrigation water is of good quality it brings appreciable amounts of sodium salts on the land. None, or practically none, of this introduced material is washed from the soil by drainage and, presumably, the continued introduction of sodium salts will, in the course of time, injure the soil and hinder crop growth unless something is done to check or reverse the process. A close watch has accordingly been kept for signs of soil deterioration, and it is satisfactory to note that hitherto no adverse cumulative change in the physical properties of the soil has been detected. Careful statistical analysis (Crowther, E. M. & F. 1935) of cotton yields from a representative area, irrigated under commercial conditions during the period 1917-31, has failed to establish a significant decline in fertility, and it is concluded that any change must be slow. This does not, of course, warrant a relaxation of our efforts, for soil deterioration, at first imperceptible, might later prove to be disastrously rapid.

It has long been recognized that the effect of sodium salts in raising the osmotic pressure of soil water and thereby making it less available for plants is, in the case of clay soils, of less importance than their effect on the soil itself. The physical state of clay soils is largely determined by their content of exchangeable bases. The soil of the Gezira already contains sufficient exchangeable sodium to behave as a sodium soil; the resulting undesirable physical properties are emphasized by increase in exchangeable sodium and are progressively reduced by decrease of exchangeable sodium. The problem of soil deterioration and soil improvement is therefore largely one of base exchange. In spite of the attention

paid to it in all parts of the world this subject unfortunately remains obscure. There are many methods of estimating exchangeable bases which adequately discriminate between different kinds of soil, but there is none which can be relied upon to provide an accurate account of the changes which occur when Gezira soil is irrigated with water drawn from the Blue Nile. It has been found (Eaton & Sokoloff, 1935; Greene, 1935) that base exchange between soil and a salt solution is affected by the soil-water ratio, and we are continuing our studies along these lines in order to extrapolate from laboratory conditions to those in the field. As a temporary expedient, we have adopted for analytical purposes a modification of Vageler's technique (Vageler & Woltersdorf, 1930), in which separate estimates are made of water-soluble bases and bases which yielded to solution after treatment with two different amounts of a displacing salt (ammonium chloride). Results so obtained are in general agreement with other conventional methods of estimation and show that in Gezira soil exchangeable bases are present to the extent of about 1 milli-equiv./g. of clay or 60 milli-equiv./100 g. of soil. The percentage composition by milli-equivalents of exchangeable bases in Gezira soil is illustrated by the following figures. Data for the freely permeable, flocculated and very fertile clay soil of the Gash Delta are included for comparison.

	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
Calcium	78	75	75	73	76	70	83	83
Magnesium	12	12	12	12	12	13	13	14
Sodium	8	11	10	13	10	15	2	2
Potassium	2	2	2	2	2	2	2	2

(a) Analyses by H. E. Cox, top foot Gezira samples.

(b) Analyses by H. E. Cox, but including water-soluble bases.

(c) Analyses by Vageler & Alten (1932) (corrected), top foot Gezira samples.

(d) As (c), but including water-soluble bases.

(e) Analyses by H. E. Cox, exchangeable plus water-soluble bases in top foot samples from Gezira Research Farm.

(f) Analyses by H. E. Cox, exchangeable plus water-soluble bases in second foot samples from Gezira Research Farm.

(g) Analyses by Vageler & Alten, ten samples from the Gash Delta, exchangeable bases.

(h) Analyses by H. E. Cox, two samples from the Gash Delta, exchangeable bases.

The figures quoted suggest that in the case of surface Gezira soil:

(a) Reduction of exchangeable sodium to about 5% of the total exchangeable bases (i.e. nearer the figure for Gash soil) would bring about a marked improvement in the physical properties of the soil.

(b) Increase over 15% (i.e. to the figure for second foot soil which physically is much poorer than the surface soil) would constitute a serious deterioration.

Our field experiments in soil improvement were first directed to the

use of gypsum and similar chemical reagents. These materials were applied in relatively small amounts of a few tons per acre in the hope that they would displace sodium and so increase the permeability of the upper soil as to permit much water to reach the salty and flocculated subsoil and so set up progressive leaching. It was found, however, that although increased penetration of water and better growth of cotton attended these treatments no deep leaching took place, and the initial increases in cotton yield were not maintained. Tests are now being made with repeated and heavier applications in conjunction with drainage.

Surprise has been expressed that so obvious a means of soil improvement as subsoil drainage was for many years omitted from our experimental work. It was, in fact, the marked low permeability of Gezira soils and the apparent impracticability of subsoil drainage that led to experiments with chemical improvers, and it was immediately established that even after heavy application of gypsum movement of water through the soil was narrowly restricted. This low permeability to water is, of course, an alarming feature of the soil; and, in seasons when the cotton yield is bad, one of the first suggestions to arise is that the soil is or has been waterlogged. It is, however, probably a mistake to consider soil conditions only in seasons of low yield; and, since a general relation has been established between cotton yields and rainfall preceding and during growth of the crop (Crowther, E. M. & F. 1935), it is better to state the problem in the following form. Is the soil the medium through which the rains exercise their main adverse effect (presumably by setting up anaerobic conditions within the root zone of the crop), or is the damage chiefly due to causes such as the carrying over of insect pests from one season to another, the delaying of agricultural operations such as sowing and weeding, and the spreading of the troublesome Blackarm disease?

Some information on this question is given by an experiment carried out at the Gezira Research Farm. Two trainloads of freely permeable soil were brought from the Gash Delta and placed in pits, 2 m. deep and provided with sump pits for bottom drainage. Cotton has been grown on this imported soil which has been sown and watered at the same time and in the same manner as adjacent plots of undisturbed Gezira soil. At no time has water drained into the sump pits, so that the imported soil has not suffered from waterlogging in any ordinary sense of the word. The imported soil has given taller plants and greater yields, presumably as a consequence of its better physical condition and of the greater depth of soil available for root growth. Over six seasons, yields from the imported soil have shown variations significantly

correlated with those from the adjacent control plots and almost significantly correlated with mean yields for six large areas in which the same type of cotton was grown under commercial cultivation.

Had the imported soil, year after year, maintained a high and fairly constant level of yield it would have been concluded that yield variation in the Gezira depended on some specific feature of Gezira soil which was not present in the imported soil. Since this is not the case the natural inference is that yield variation in the Gezira cannot easily be ascribed to soil conditions but is mainly due to variations in pests and disease or to some cause not yet recognized. This inference, however, should be regarded with caution. The correlation between yield variations is not firmly established, and, since the plots of imported soil are small, it is possible that plants growing on them have been indirectly affected by changes induced by rain in the adjacent Gezira soil. With this reservation the experiment seems to constitute a partial resolution of the problem.

Our field experiments in subsoil drainage have not shown promise of any wide-scale improvement that is commercially practicable. They include trials with and without soil improvers and are described below. In work of this kind the aim is to establish progressive soil improvement extending laterally from the immediate vicinity of the drains, and we have found that the initial effect, at any rate, is so narrowly localized that a costly drainage system would be needed to achieve any quick result. One has to bear in mind that with normal irrigation only a fairly shallow layer of soil is moistened and there is very little water that could be removed by drains. The average level of yield (Sakellarides type) in the Gezira is moderately high and compares favourably with that in Egypt. Seedlings of cotton and sorghum in the first few weeks of growth are liable to injury from overwatering, and this danger is readily met by provision of surface drains to remove storm water. As soon as the plants are established however, it is surprisingly difficult to depress the yield by giving too much water, and there is accordingly little inducement to install an elaborate system of subsoil drainage.

Apart from what may be broadly described as attempts to remove exchangeable sodium by chemical and mechanical means we have experimented also with a biological agent. This third and perhaps more promising line of attack attempts improvement within the soil by growing plants which take up large amounts of sodium. Analyses of salt-bush grown under field conditions are now presented. The figures are of interest in demonstrating a commercially practicable procedure for preventing the accumulation of sodium salts brought on to the land by

the irrigation water. This is very satisfactory although we have yet to establish that, without some special measures of this kind, the general tendency of normal irrigation is to promote a slow accumulation of salts rather than a slow downward displacement through the soil column.

While this work was in progress it seemed desirable to repeat and extend previous analyses of irrigation water. The data are reported in § IV.

I. USE OF CHEMICAL REAGENTS IN FIELD TRIALS

A. *The purpose of soil improver trials*

W. Beam (1911) first recommended the application of gypsum to Gezira soil. The use of substances such as calcium chloride, gypsum, sulphur, sulphuric acid, ferrous sulphate and aluminium sulphate is a recognized remedy for such conditions, but is ordinarily combined with copious watering which removes from the soil column the sodium and other salts which result from chemical reaction between the soil and the improver. In the Gezira we have failed to increase the permeability of the soil to an extent that permits this washing away of salts: this difficulty had been foreseen, but the experiments were tried in the hope that the soluble products of reaction would be washed down sufficiently far to make contact with the saline subsoil and so possibly establish partial drainage.

The following sections describe the effect of soil improvers on cotton yield, moisture content, nitrogen supply and salt content of the soil.

B. *Effect of soil improvers on cotton yield*

(1) *Experiments with gypsum and ammonium sulphate.*

In seasons 1927-8, 1928-9 and 1929-30 gypsum (4 tons, 2 tons and none per acre), with and without ammonium sulphate (200 lb./acre applied 6 weeks after sowing), gave yields (reckoned in each case on three randomized blocks) as shown in Table I. Yields are given as kantars per feddan, which roughly equal hundreds of lb. cotton lint/acre.

Table I. *Immediate effect of gypsum*

Season ...	1927-8			1928-9			1929-30		
Amm. sulphate ...	0	200	Diff.	0	200	Diff.	0	200	Diff.
Gypsum: 4 tons	4.11	4.35	0.24	4.04	4.72	0.68	2.37	2.84	0.47
2 tons	3.95	4.20	0.25	4.10	4.84	0.74	2.39	2.79	0.40
None	2.71	3.78	1.07	2.88	3.74	0.86	2.22	2.78	0.56
Av. yield Gezira	3.29			3.55			2.12		

Standard error of treatment means 2.8%.

In the three subsequent seasons no further addition of gypsum was made but ammonium sulphate was applied as before. Results are given in Table II.

Table II. *Residual effect of gypsum*

Season	1930-1			1931-2			1932-3		
	0	200	Diff.	0	200	Diff.	0	200	Diff.
Amm. sulphate ...									
Gypsum: 4 tons	1.36	1.68	0.32	3.29	4.18	0.89	1.85	2.14	0.29
2 tons	1.33	1.67	0.34	3.30	4.31	1.01	1.81	2.05	0.24
None	1.38	1.57	0.19	2.99	3.89	0.90	1.73	2.08	0.35
Av. yield Gezira	1.30			4.04			1.91		

Standard error of treatment means 2.2%.

Gypsum markedly increased the yields in the two seasons of high average yield but not in 1929-30. The residual effects of gypsum were small, especially in the two seasons of low yield. Sulphate of ammonia consistently improved yields, though the responses varied significantly with season. In each of the experiments the response to sulphate of ammonia was greatest in the absence of gypsum, though the differences were small in two of the three years and the interaction was not statistically significant.

(2) *Experiments with different soil improvers and ammonium sulphate.*

In seasons 1930-1 and 1931-2 rather more elaborate experiments were carried out with results described below. In the *latter* season an area of 10 acres was divided into forty subplots which provided eight replicates of five improver treatments, and one-half of each subplot received in addition ammonium sulphate (400 lb./acre) applied 6 weeks after sowing. Yields (kantars per feddan) were as in Table III, which also includes the residual effects in season 1934-5.

Table III.

		Yields with and without N				Response to N 1931-2
		1931-2		1934-5		
Treatment	Tons/acre	O	N	O	N	
Potassium sulphate	2.00	3.92	4.21	4.42	--	0.29
Sulphur	0.375	2.94	3.52	4.40	--	0.58
Control	--	2.57	3.48	4.21	--	0.91
Gypsum	2.00	3.38	3.97	4.36	--	0.59
Ferrous sulphate	3.25	3.79	4.15	4.22	--	0.36
Average Gezira		4.04		4.33		

Standard error of treatment means in 1931-2, 5.58%.

Nitrogen was found to have, as usual, a highly significant effect. Soil improver effects were also significant, potassium sulphate, ferrous

sulphate and gypsum being significantly superior to control whereas sulphur was not. Three years later the experimental area was halved and showed small residual effects from soil improvers, no ammonium sulphate being applied.

The similar experiment carried out in season 1930-1 gave the results shown in Table IV.

Table IV. *Immediate and residual effects of various improvers*

Treatment	No. of subplots	Mean yields with and without N		Response to N	
		1930-1	1933-4	1930-1	1933-4
Gypsum	8	2.89	2.52	0.74	0.68
Calcium chloride	4	2.95	2.46	0.67	0.63
Ferrous sulphate	8	3.00	2.56	0.59	1.01
Sulphur	8	2.73	2.53	0.51	1.06
Control	12	2.30	2.40	0.98	1.16
Average Gezira		1.30	2.31		

(3) *Four-factor experiment with gypsum, sulphate of ammonia, sowing date and spacing.*

In season 1930-1 two four-factor experiments were carried out at the Gezira Research Farm. Yields throughout the Gezira were the lowest yet recorded, and it was interesting to find that no combination of treatments raised yields to the level of a moderately good season. One of these experiments was designed to test the effects of sowing date, spacing, nitrogen and water on cotton yield and has been fully described by Gregory *et al.* (1932). The other experiment, carried out by Greene *et al.* was similar in design, but the watering differences were regulated by application of gypsum instead of being directly regulated. The two experiments gave closely concordant results showing that application of gypsum had had the anticipated effect of allowing the soil to take up more water at each irrigation. Minor differences between the two sets of data were also consistent and suggested that plants suffered from a more severe shortage of nitrogen in the experiments of Gregory *et al.* than in that for which yields are now given (Table V). This conclusion cannot be supported by statistical evidence, nor is it established that the general low level of yield was due to root trouble which nevertheless is not unlikely.

Sowing date, nitrogen, gypsum and spacing were all highly significant, as were the interactions sowing date *v.* gypsum and sowing date *v.* spacing. No other interactions were significant. August sowing was significantly superior to September sowing, nitrogen to no nitrogen and gypsum to

no gypsum. Differences between 300 and 600 lb./acre ammonium sulphate were not significant, nor those between 2 tons and 4 tons gypsum. Gypsum produced large effects with early sowing but small and even depressing effects with late sowing. This resembled the results obtained directly by different levels of watering except that depression of yield was not shown. This effect, therefore, may be of a different character, and it is possible that in the hot September weather seedlings were injured by a local concentration of sodium sulphate. Close spacing was most advantageous with the August sowing and least with the July sowing.

Table V. *Season 1930 -1. Data obtained by Greene et al.*
Yields in kantars per feddan

Amm. sulphate ...	No gypsum			2 tons gypsum			4 tons gypsum		
	0	300	600	0	300	600	0	300	600
Sown 22 July:									
Spacing 35 cm.	1.79	2.12	2.41	2.17	2.72	2.92	2.13	2.70	2.82
Spacing 70 cm.	1.52	2.20	2.41	2.09	2.40	2.45	2.11	2.17	2.57
Sown 22 Aug.:									
Spacing 35 cm.	2.34	2.71	2.86	2.36	2.70	3.10	2.71	3.04	3.31
Spacing 70 cm.	2.08	2.21	2.12	2.08	2.28	2.36	2.41	2.42	2.51
Sown 22 Sept.:									
Spacing 35 cm.	1.46	1.61	1.88	1.60	1.77	1.97	1.19	1.80	1.58
Spacing 70 cm.	1.16	1.39	1.72	1.34	1.45	1.61	0.88	1.60	1.33

Standard errors: sowing date 14.2, nitrogen 2.8, gypsum 2.8, spacing 1.1%.

C. *Effect of soil improvers on moisture content of the soil*

Greene (1928) has described an experiment in which application of gypsum to soil of low permeability led to increased penetration of water. This observation has been amply confirmed by other experiments:

(1) In one case 3 and 14 days' flooding were given to small squares with and without a dressing of gypsum at the rate of 12.5 tons/acre. Table VI shows percentage moisture contents before and after flooding: with gypsum the amount of water taken up is increased and its distribution is more even.

Table VI. *Percentage moisture contents of soil*

Depth ft.	Before flooding	3 days' flooding		14 days' flooding	
		Gypsum	Control	Gypsum	Control
1	13.8	32.3	35.6	31.5	33.5
2	17.9	31.1	32.1	31.9	33.4
3	18.8	30.2	25.9	31.5	31.9
4	21.6	29.0	23.0	33.3	26.2
5	22.1	22.8	22.0	32.7	21.9
6	21.3	21.5	21.4	29.1	21.0

(2) In an experiment designed to test methods of application, (a) gypsum in coarse crystals, (b) the same material finely ground, and (c) plaster of Paris, were applied in chemically equivalent amounts and at the rate of 2 tons gypsum/acre. The depths to which water had penetrated after 1 week's flooding were roughly as follows:

Table VII.

	in.
No gypsum	42
Gypsum (coarse crystals)	57
Gypsum (finely ground)	57
Plaster of Paris	63

The small difference in favour of plaster of Paris may be ascribed to the more ready solubility of this substance.

(3) In another experiment gypsum and potassium sulphate applied in equivalent amounts gave practically identical increases in water penetration.

(4) The following results (in Table VIII) were obtained in October 1929, after exceptionally heavy rains and artificial flooding for 1 week, in a comparison of the action of sodium sulphate, potassium sulphate and gypsum with control. They also indicate that the increased penetration is due in part to the flocculation of salts and not wholly to base exchange.

Table VIII. *Percentage moisture content of soil*

Treatment	Sodium sulphate	Control	Gypsum	Potassium sulphate
1st foot	33.2	31.9	30.4	27.4
2nd foot	34.0	32.7	31.4	29.0
3rd foot	33.0	30.8	30.9	29.7
4th foot	32.6	31.3	32.3	32.0
5th foot	32.2	30.9	32.2	32.5
6th foot	28.9	27.6	30.4	30.1

It appears that water penetration was deeper in subplots receiving sodium sulphate than in control plots, but not so deep as in those receiving gypsum and potassium sulphate.

The plots had been allowed to dry a little before the samples were taken, and the rates of drying out appear to have stood in the order: potassium sulphate, gypsum, control and sodium sulphate. This suggests that in the subplots treated with sodium sulphate there was at first increased penetration of water due to flocculating action of the salts, and that thereafter the surface soil, enriched in exchangeable sodium, became more sticky and held its water more firmly than the untreated and improved soils.

(5) Results obtained when soil improvers are applied to land about to bear a cotton crop are sufficiently illustrated by Fig. 1, which represents

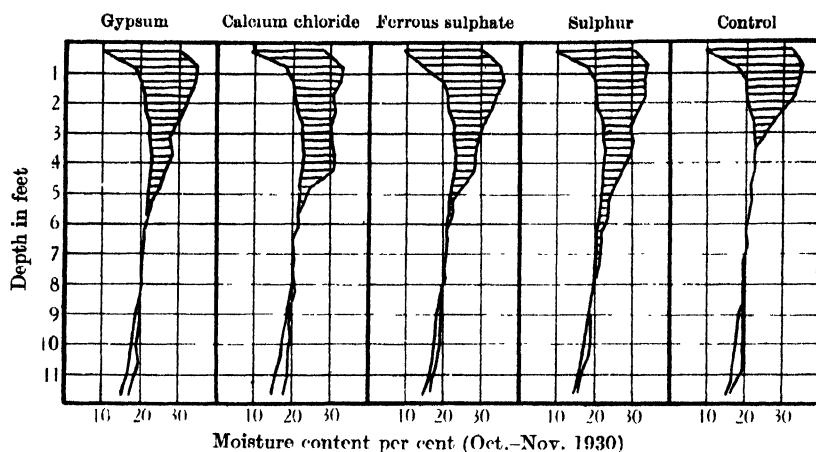


Fig. 1.

the moisture content of plots for which yield data are given in Table IV, season 1930-1. The left-hand curves show the moisture content of unwatered soil.

D. Effect of soil improvers on nitrogen supply

It is to be expected that soil improvers, by conferring a more open structure on the surface soil, should increase the nitrogen supply for the plant as well as the supply of available water. In this case it would follow from the law of diminishing returns that soil improvers and nitrogenous manures would be more effective singly than together. Although, in individual experiments, this expected interaction of soil improvers *v.* nitrogen has not reached the 5% level of significance, the data assembled in Table IX (abstracted from Tables I, III and IV) show that single dressings were relatively more effective in each of the five seasons for which figures are available.

Table IX. *Yields in kantars of seed cotton per feddan*

Season	Lb./acre sulphate of ammonia	Untreated yield	Response to nitrogen		Response to improver	
			With improver	Without improver	With nitrogen	Without nitrogen
1927-28	200	2.71	0.24	1.07	0.49	1.32
1928-29	200	2.88	0.71	0.86	1.04	1.19
1929-30	200	2.22	0.44	0.56	0.04	0.16
1930-31	400	1.81	0.63	0.98	0.41	0.76
1931-32	400	2.57	0.45	0.91	0.48	0.94

The effect of increasing doses of sulphate of ammonia on cotton yield (kantars of seed cotton per feddan) are quoted, in Table X, from the reports of the Agricultural Section of this Service (1932-3 to 1936-7).

Table X.

Doses, sulphate of ammonia, lb./acre

		0	200	400	600	800	
1932-33	Sakel	2.09	2.65	3.23	3.40	4.07	Repeated
1933-34	Sakel	2.62	2.91	3.19	3.23	3.30	..
1934-35	X 1530	6.00	6.27	6.62	7.26	7.62	..
1935-36	X 1530	5.39	6.26	6.80	7.58	—	Single
1936-37	X 1530	5.99	6.92	8.12	8.33		..

With Sakel cotton, the variety used in all our improver experiments, there are diminished returns on the heavier applications.

The effect of gypsum on nitrogen supply is confirmed by observations on soil nitrates carried out in seasons 1927-8 and 1928-9 on the plots for which yield data are given in Table I. The results are given in Tables XI and XII, each figure being the mean of two or three determinations.

Table XI. *Plot 28, season 1927-8. P.p.m. nitric N in top foot composite samples from ridges*

Treat- ment	Gypsum	Ammonia sulphate	Sept	Oct	Nov.	Dec	Jan	Feb.	Mar.	Apr.	Mean
1	4 tons	None	6	6	6	7	3	2	9	7	6
2	2 tons	None	3	6	7	6	4	13	18	7	8
3	None	None	13	7	5	2	4	3	9	4	6
4	4 tons	200 lb.	4	10	10	9	5	7	11	4	8
5	2 tons	200 lb	7	18	22	16	16	9	4	3	12
6	None	200 lb	19	13	13	13	6	5	5	3	10

Table XII. *Plot 74, season 1928-9. P.p.m. nitric N in top foot composite samples from ridges*

(Treatments as in Table XI)

Treat- ment	May	June	July	Aug.	Sept	Oct.	Nov.	Dec	Jan	Feb.	Mar.	Apr.	Mean
1	4	7	6	-	14	6	12	24	17	13	17	7	12
2	6	6	7	5	12	13	15	44	8	37	10	12	15
3	6	6	6	15	10	6	14	13	6	26	6	7	10
4	4	5	7	12	10	15	47	23	58	52	21	9	22
5	5	6	6	13	16	7	44	54	39	28	51	11	23
6	6	5	6	—	16	7	45	46	33	13	17	14	19

Although the results in these two tables are far from consistent it seems evident that nitrification of ammonium sulphate proceeds normally on soil treated with gypsum; and also that, although higher yields were obtained from subplots treated with gypsum (so that consumption of nitrates by the plants was presumably higher), yet the

amount of nitrate left in the soil was on the whole rather above that of subplots receiving no gypsum.

No observations have been made as to the effect of calcium chloride, ferrous sulphate or potassium sulphate on nitrification, but it is presumed that these substances do not differ greatly from gypsum. Sulphur, on the other hand, gives rather disappointing returns in respect to yield, and this was traced to slowing down of nitrification. In a series of pot experiments, which, by courtesy of the Director, were carried out at Rothamsted Experiment Station, mixtures of Gezira soil (200 g. air dry) with and without sulphur (0.1 g., which equals about 0.75 tons/acre reckoned on the top foot of soil) were moistened with 60 c.c. water or an equal volume of solutions containing calcium cyanamide (0.33 g./litre) or ammonium sulphate (0.30 g./litre). Estimations of nitrate, ammonia, and soluble salts were made 2, 8, 29 and 73 days after beginning of incubation; it appeared that the ammonia content of the soil decreased with time and, in the case of soil treated with sulphur, the soluble salt content rose—thus showing that oxidation of sulphur, under the conditions of the experiment, required 2 or 3 months for completion. The nitrate results are given in Table XIII.

Table XIII. *Nitric N p.p.m.*

Days	S	S + CaCN ₂	S + Sulph. amm.	Control	CaCN ₂	Sulph. amm.
2	5	4	5	5	5	5
8	6	3	11	15	12	15
29	11	17	22	23	18	25
73	14	47	45	37	51	70

The results show that sulphur strongly retarded nitrification in soil receiving no added nitrogen and slightly retarded nitrification in soil to which calcium cyanamide or ammonium sulphate had been added.

E. Effect of gypsum on soil salts

When Gezira soil is treated with gypsum and is watered, sodium sulphate (together with a certain amount of magnesium and potassium sulphates) is produced in approximately the theoretical amount. Table XIV shows increases in salt content of the top 2 ft. of soil as observed in certain field experiments, the determinations being conductimetric.

Complete conversion of gypsum to sodium sulphate ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$ to Na_2SO_4 , on a weight basis) would increase the salt content by 82.5 % of the amount of gypsum added as against the 83, 84 and 86 % shown above. Although this close agreement is due, in part, to balanced errors,

Table XIV. *Increases in salt content of soil after application of gypsum (per cent on soil)*

Amount of gypsum applied per acre ...	4 tons	2 tons	1 ton
Plot 28	0.113	0.060	—
Plot 52, square $V_3V_4V_5$		0.046	—
Plot 52, square VIII 2	0.094	—	—
Manurial trials	—	—	0.027
Mean %	0.104	0.053	0.027
Mean as tons per acre	3.31	1.68	0.87
Mean as percentage of amount applied	83	84	86

there is no reason to doubt that sodium and other sulphates are produced in chemically equivalent amount when gypsum reacts with soil, nor that these salts are initially located in the top 2 ft. of soil. As irrigation proceeds sodium sulphate is washed down from the surface layers of soil. Table XV shows results obtained for the top 2 ft. of a plot which had been treated with gypsum and gave the yields shown in Table I for season 1927-8.

Table XV. *Salt content per cent*

Treatment	Month . Year ..	Aug 1927	Feb. 1928	Apr. 1928	Oct. 1928	Apr. 1929
No gypsum top foot		0.10	0.10	0.11	0.09	0.07
No gypsum second foot		0.10	0.11	0.11	0.09	0.10
2 tons gypsum top foot		0.20	0.24	0.13	0.09	0.08
2 tons gypsum second foot		0.16	0.17	0.16	0.11	0.14
4 tons gypsum top foot		0.27	0.26	0.18	0.12	0.10
4 tons gypsum second foot		0.18	0.16	0.16	0.14	0.15

In this experiment gypsum was applied in June 1927; rain amounting to 344 mm. fell in July, August and September. The plot was watered in August 1927 and sown 18 August, and twelve further waterings were given in the period September 1927 to April 1928—when the crop was cut out. The soil then lay bare for 3 months. The summer rains of 1928 amounted to 319 mm. of which more than half fell in August. Sorghum was sown in August and harvested in November, and thereafter the soil was again allowed to lie bare.

Fig. 2 gives results obtained in three samplings of plot 74 which in season 1928-9 carried a repetition of this experiment. The dotted lines show salt contents prior to application of gypsum; the white circles represent salt content in September 1928, that is, early in the cotton season, and the black circles give contents in April 1929, that is, at the end of the cotton season. Displacement of salt (sodium sulphate) from the surface is clearly shown in the diagram, which has additional interest in demonstrating the satisfactorily concordant results obtained by

taking a large number of samples. It will be noticed that the subsoil salts seem to have been displaced downwards as a result of irrigation. This is really a consequence of swelling and mechanical disturbance of the surface layers and is no true movement of salts through the soil mass.

The following remarks may be made on these data. Treatment of Gezira soil with solutions of either calcium sulphate or sodium sulphate causes displacement of, mainly, sodium and calcium respectively. The observations recorded above probably represent in the last stages an amelioration of the surface soil by the gypsum, and a reverse effect in the second or third foot of soil which receives the sodium displaced from the surface. This secondary reaction implies a production of gypsum. If it occurs, as may be the case, in a zone of soil which already contains

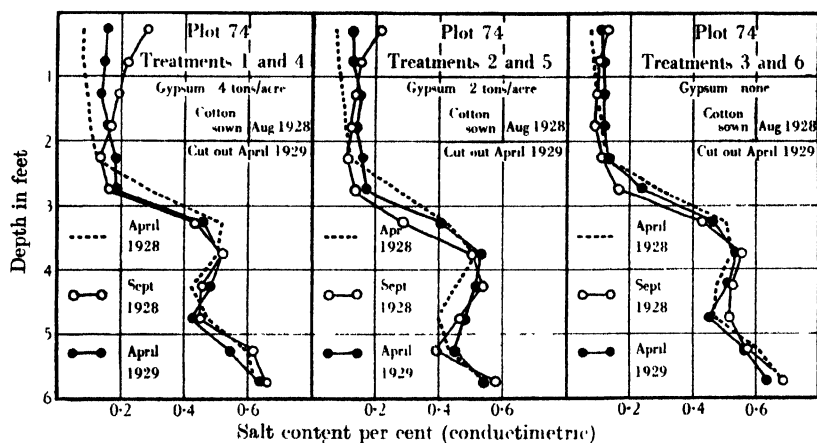


Fig. 2.

gypsum there will be a decrease in the apparent salt content of the soil column, since gypsum is sparingly soluble and is not adequately estimated by 5 to 1 extraction. Thus, although application of gypsum is followed at first by an increase in salt content (which agrees closely with that expected), there ensues a reduction in apparent salt content. To follow the changes in greater detail would necessitate repeated and accurate analyses for which we have not yet found time.

Since sodium sulphate has been found to increase water penetration (para. C (4) above), and since the residual effect of soil improvers is small by the time that sodium sulphate, formed by interaction of soil and soil improver, has been washed down from the surface soil, it seems likely that a considerable part of the initial response to soil improver is due to flocculating action of the salts applied to or formed in the surface layer.

II. DRAINAGE EXPERIMENTS

An informal and lively discussion on subsoil drainage in the Sudan Gezira is contained in nos. 1, 2, 3 and 4 of the *Empire Cotton Growing Review* for 1935 (Balls, Barritt, Dempster, Greene & Bailey, and Roberts). It has not been possible to act upon all the suggestions then made, but some small-scale experiments have been carried out and have provided new data.

The experiments include (A) subsoil drainage from undisturbed soil, (B) subsurface drainage with and without soil improvers and (C) subsoil drainage from a cotton plot.

A. Subsoil drainage from undisturbed soil

The soil returned to a trench in which drains have been laid is usually looser than undisturbed soil, and the time it takes to settle is, to some degree, a matter of chance. An unexpectedly large effluent may be obtained if, at some point, irrigation water has almost direct access to the drain. To meet this difficulty we used a specially designed and rather clumsy boring apparatus to drive horizontal bores at a depth of 2 ft. below the soil surface of two small plots of which one received gypsum at the rate of 10 tons/acre. The bores were 3 in. in diameter and 2 m. apart, each small plot being served by four bores. Perforated iron pipes were inserted in these bores and were packed externally with coarse sand. Two undrained plots for comparison were adjacent. When the plots were kept continuously under water for 8 weeks the average effluents were as follows:

Control plot	...	1.8 m. ³ /feddan/day
Treated plot	...	6.2 m. ³ /feddan/day
(1 feddan = 4200 m. ² = 1.038 acres).		

During the period of this experiment the amount of water applied to make good loss by evaporation was estimated at about 56 m.³/feddan/day. It appeared therefore that (1) even under the most favourable conditions only small effluents can be obtained from untreated, undisturbed soil, and (2) application of gypsum at the soil surface notably increases effluents to be obtained at 2 ft. depth.

B. Subsurface drainage with and without soil improvers

Two reasons for the unsatisfactory results of soil improver experiments (§ I above) are the use of insufficiently heavy applications of the chemical reagent and failure to remove the soluble products of reaction.

As subsoil drainage is difficult it was decided to attack the second difficulty by constructing drains unusually close to the soil surface. For this purpose trenches 2 ft. deep and 1 ft. wide were dug. In them, burned bricks were placed forming a tunnel $3 \times 4\frac{1}{2}$ in. internally and 9×9 in. in external section. The bricks overlapped so as to have maximum

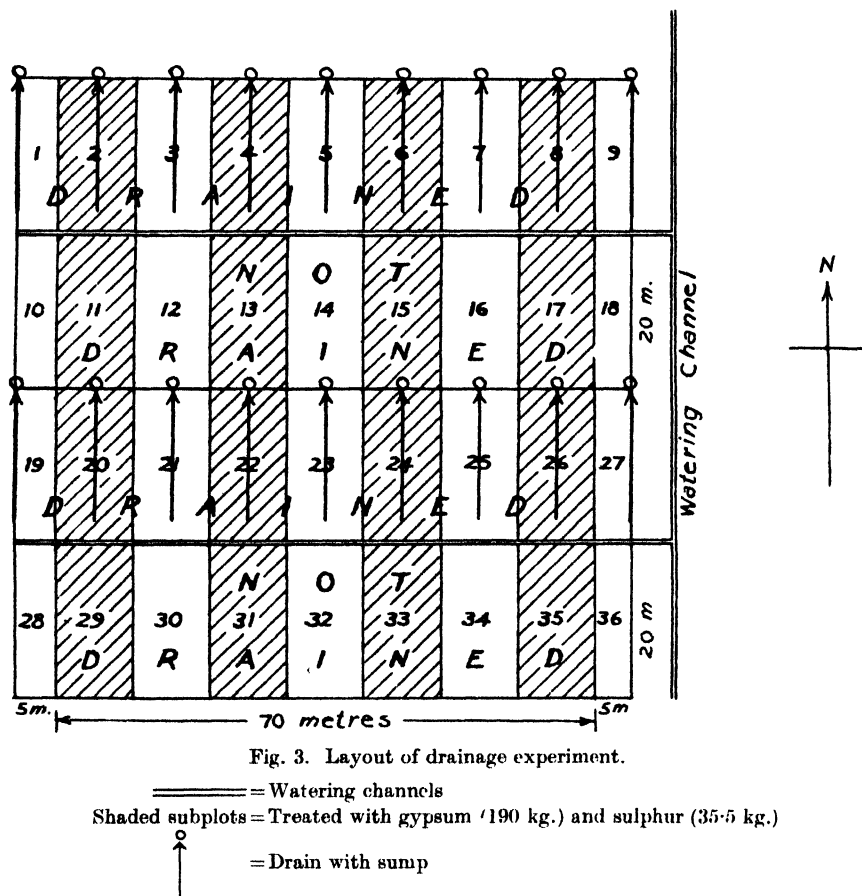


Fig. 3. Layout of drainage experiment.

stability in case of vertical displacement of soil occasioned by change in moisture content. The trenches were then filled with coarse sand to within 6 in. of the surface and the remaining space was filled with soil, excess soil being removed to form banks along the subplot boundaries.

The lay-out of the experimental area is shown in Fig. 3. The unit plots are 10×20 m., arranged in four rows of which two are provided with independent subsurface brick plus sand drains emptying into sump

pits baled out by hand. To avoid a long carry waste pipes were provided for disposal of the effluents. No excavation was done on the undrained subplots. Gypsum and sulphur were applied as shown, giving four soil treatments:

- (1) Soil improvers with drainage.
- (2) Soil improvers without drainage.
- (3) Untreated soil with drainage.
- (4) Untreated soil without drainage.

The whole area has been flooded for periods of 3 and 4 weeks with long dry intervals. With continued watering large effluents were obtained from the drains. A record of these volumes was kept and samples were taken for analysis.

(a) *Water duties and effluents.*

No equipment for measuring irrigation water applied was available. By keeping a free water surface on the subplots and by use of screen Piché data an estimate of loss by evaporation¹ was obtained; soil moisture samplings gave a measure of the water taken up by the land; these two measurements plus drainage gave a measure of the water applied. Analyses of the irrigation water and of the effluents enabled a balance sheet to be made. As a matter of convenience the north and south halves of the area were watered at different times.

The observations in Tables XVI and XVII were made in four experiments, the figures being m.³ per subplot.

Table XVI.

Period of flooding in days ...	Exp. I A, south half Jan.-Feb. 1936 30-33		Exp. II A, north half Feb.-Mar. 1936 19	
	Gypsum + sulphur	Controls	Gypsum + sulphur	Controls
Soil treatment				
Water held by soil	110	80	110	80
Water evaporated (calc.)	72	73	54	54
Effluent from drains	135	63	138	135
Total water used	317	216	302	269

The effluents from the treated subplots of Exp. I A were considerably greater than those from the controls, whereas in the other experiments the differences were smaller. This was due to hydrostatic effects. In Exp. I A the land was watered for the first time after application of soil improvers and the subplots started at the same level. The north

¹ Taken as 58% of evaporation from Piché tube in our standard screen (Sutton, 1923).

Table XVII.

Period of flooding in days ...	Exp. I B, south half Jan. 1937 17-18		Exp. II B, north half Nov.-Dec. 1936 17-19	
	Gypsum + sulphur	Controls	Gypsum + sulphur	Controls
Soil treatment				
Water held by soil	44	51	44	51
Water evaporated (calc.)	33	34	40	41
Effluent from drains	109	69	125	104
Total water used	186	154	209	196

strip (Exp. II A) had received a part of its soil improvers and had been watered in an earlier trial, and in consequence of differential uptake of water accompanied by swelling of the soil the treated subplots stood about 6 cm. higher than the control subplots. During the present experiments the latter were accordingly standing under a greater head of water. Similar differential effects were observable in Exps. I B and II B.

The total amount of water applied in these experiments was about 10,000 m.³/feddan. In the course of a complete season cotton receives about 6000 m.³/feddan. Smaller effluents would be expected with intermittent watering as in normal irrigation of cotton. Evaporation varies considerably through the year, an important point if flooding is ever carried out on a large scale.

The subsoil took up a good deal of water during the first long watering (series A) but did not dry out to any extent during the 8-12 months intervening before the second long watering (series B) and accordingly was less affected on the second occasion. The observations are given in more detail below.

(b) *Chemical analyses.*

Composites of the effluents and of the irrigation water applied were examined for various constituents, of which calcium, magnesium, sodium, and sulphate ions and alkalinity are the most important. In addition the removal of salts in Exp. I A was followed very closely. Notes on the composition of the irrigation water will be found in § IV.

Table XVIII gives the amounts in kilograms of various ions (a) introduced by improvers and with the irrigation water, and (b) removed by the drains. The improver treatment corresponds to 44.2 kg. calcium and 212.5 kg. sulphate ions per subplot. Alkalinity is expressed as bicarbonate ion, although part is due to silicates.

It was subsequently established that the drains effectively serve only a narrow strip of soil immediately adjacent to them and not the 10 m.

width of subplot. A part of the leachate from the soil improvers soaked past the drains, and these figures do not strictly correspond with laboratory data on base exchange in which the leachate is obtained by convenient filtration. It is interesting to note, however, that in both treated and untreated subplots calcium and magnesium are extracted from the irrigation water, and sodium is lost from the soil. This is consistent with the known easy replaceability of exchangeable sodium.

Table XVIII.

Ion	Treated		Control		Treated		Control	
	+	+	+	-	+	-	+	-
		Exp. I A				Exp. II A		
Calcium	52.4	5.4	5.6	0.7	52.0	5.8	7.0	2.3
Magnesium	1.3	0.6	0.9	0.1	1.2	0.5	1.1	0.2
Sodium	4.1	13.5	2.8	5.2	3.9	13.7	3.5	8.2
Sulphate	215.3	24.5	1.9	1.7	215.2	27.3	2.6	4.7
Alkalinity	35.5	21.0	24.2	9.0	33.8	20.1	30.1	23.0
		Exp. I B				Exp. II B		
Calcium	48.7	10.8	3.7	1.2	49.0	10.7	4.5	1.8
Magnesium	0.9	0.5	0.8	0.2	1.0	0.7	1.0	0.3
Sodium	2.2	9.8	1.8	4.6	2.3	12.6	2.2	5.0
Sulphate	214.2	34.9	1.4	3.0	214.2	39.5	1.6	2.1
Alkalinity	19.0	14.1	15.7	10.9	20.5	15.6	19.2	15.1

+ Introduced by improvers and water.

- Removed by drains.

The net loss of sodium from control subplots at the end of the second watering was about 6 kg. This is about one-seventh part of the exchangeable sodium in the top 6 in. layer of soil of the subplot. The change is small but in the right direction. In the case of the treated subplots a part only (15%) of the added sulphate (including sulphur) is removed in spite of the considerable flow. Most of the calcium is probably retained by the surface soil by base exchange and the sulphate washed into the subsoil as sodium sulphate. Calcium removed from the treated subplots in the effluents is roughly equivalent to 10% of the added gypsum in series A and 20% in series B. As the surface soil becomes enriched in calcium it becomes necessary to deepen the drains and withdraw effluents at a lower level. This operation has not yet been undertaken.

The analyses show that an accumulation of acid radicals in the soil accompanied the prolonged watering and incomplete leaching. Evaporation was rapid throughout, and it is presumed that carbonates and silicates of calcium and magnesium were separating from solution.

(c) Lateral movement of water.

From the results of the above experiment it appeared that the large volume of water recovered from the drains did not effectively leach the soil but only that small part of the soil immediately adjacent to the drain and near the surface of the plot. To test the view that lateral movement of water is extremely small a strong solution of fluorescein was placed in the soil of control and treated subplots at points distant 1, 2 and 4 m. from the centre line of the drain and at a depth of 6-21 in. Examination of the effluents showed no fluorescein in the case of control subplots but was positive for treated subplots in which the dye had been placed 1 and 2 m. from the drain.

A more stringent test was applied by erecting light earth banks on either side of the drains, thereby dividing the subplots into three parts. The central part including the drain but containing no fluorescein was not watered, but the two sides having fluorescein adjacent to the earth banks were watered for 11 days. The object of this modification was to prevent dilution of the lateral effluent by the considerable volume of water entering the drains more directly. Water seeped through and under the light earth banks and gave small effluents, but, as before, fluorescein was detected only in the case of treated subplots in which the dye had been placed 1 and 2 m. from the drain.

(d) Vertical movement of water.

Under normal irrigation water penetration is sensibly limited to the few feet of soil above the salty subsoil. Deeper penetration occurs with heavy continuous flooding. Table XIX shows soil moisture contents (percentage by weight on dry soil) as determined before the first long

Table XIX. *Percentage moisture contents*

Depth in ft.	Before watering	Four weeks after second watering			
		Control		Treated	
		Drained	Undrained	Drained	Undrained
1	13	31	31	27	27
2	23	33	33	31	31
3	20	32	32	32	31
4	20	32	33	32	32
5	21	33	33	32	33
6	20	30	30	31	31
7	20	30	29	29	30
8	20	29	28	29	29
9	19	27	28	29	29
10	19	27	24	28	27
11	19	27	24	26	25
12	19	26	19	25	22

watering and after the second long watering. It will be noticed that a large amount of water has entered the soil, and that at the end of the experiment there was little difference between drained and undrained soil or between treated and untreated soil.

Differences in moisture content of the soil were, however, found at intermediate stages of the experiment as is shown in the accompanying Fig. 4, from which it will be seen that application of soil improvers permitted deeper penetration of water during the first long watering.

At the time of the second flooding almost a year later drying out had not proceeded below 5 ft. in the controls, whereas in the treated land it had begun to some extent down to 10 ft. This is presumably a consequence of the more open texture of the treated land.

As has been stated, the second long flooding almost obliterated the difference in subsoil moistures between treated and untreated land. It appears that the latter took longer to reach the same level of saturation. This level is considerably below the moisture equivalent of the soil as measured in the laboratory. Whether this level corresponds with the field moisture equivalent (i.e. of soil under pressure of the upper layers) or whether further amounts of water would slowly be taken up on continued watering we do not know.

These observations seem in general agreement with those previously reported (Greene, 1928).

C. Subsoil drainage of a cotton plot

Drains of burned brick as described above but without a covering of coarse sand were laid at about 30 in. depth to serve four strips 20 m. wide and 70 m. long in plot 124 at the Gezira Research Farm, Medani. Yields from these strips were compared with those from adjacent strips trenched to the same depth but not drained. The effluents were small, as were differences in yield due to treatment. There was, however, a marked gradient in yield which we have failed to connect with the more permanent chemical characteristics of the soil. Final yields (Sakel, kantars per feddan) were as in Table XX, the general high level being ascribed to application of nitrogen and long previous fallow. Heavy cross applications of superphosphate and potassium sulphate were given but had small effect; this result is not unexpected in view of earlier manurial trials.

Drains I, II and IV were partly exposed and cleared in September 1935. All drains were flushed out several times during the season and

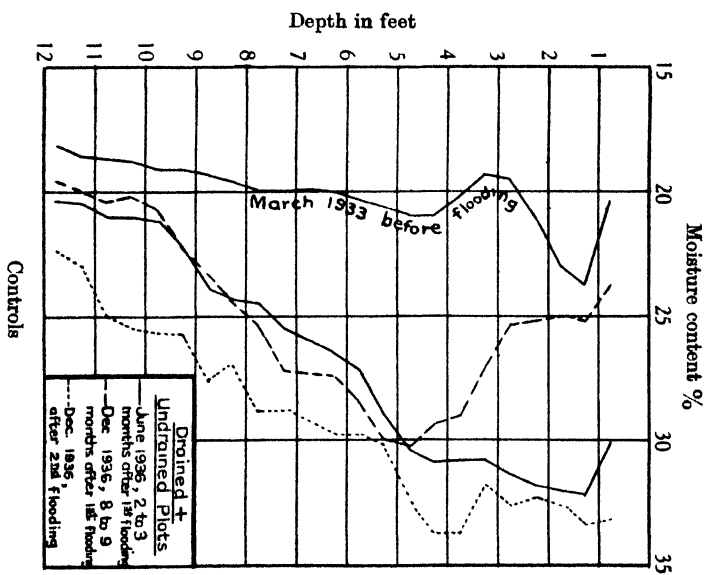
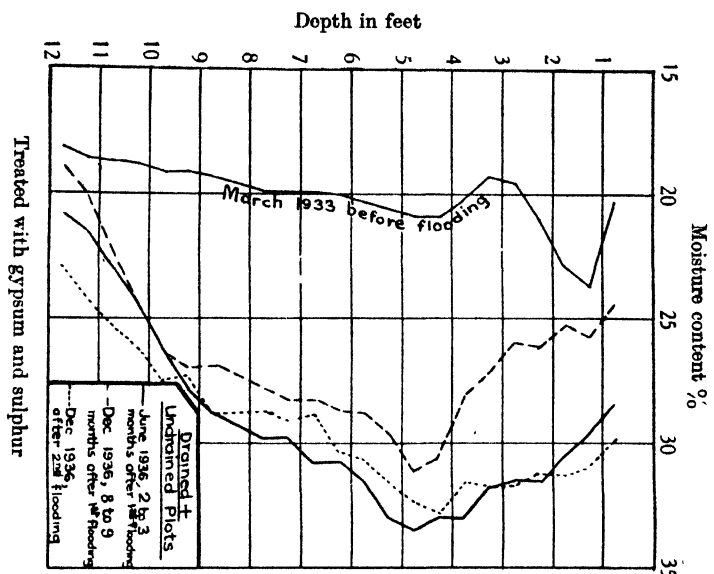


Fig. 4.

were clear at the end of it. The amount of water applied per irrigation was about 150–200 m.³ per strip.

The ratio of effluent to water applied is very small; even so, it is possible that part or much of it was due to soil disturbance and came from surface water immediately above the drain.

Table XX.

	Kantars/feddan	Average effluent (15 waterings)
South belt (no nitrogen)	3.97	
Control I	4.88	
Drain I	4.45	1.3 m. ³ (often choked)
Drain II	5.26	6.5 m. ³ (choked at first only)
Control II	5.09	
Control III	5.26	
Drain III	5.66	3.0 m. ³ (regular, not choked)
Drain IV	6.20	1.1 m. ³ (choked at first only)
Control IV	6.68	
North belt (no nitrogen)	3.51	
Average of controls	5.48	
Average of drained	5.39	

As the action of the drains seemed narrowly localized, yields were taken not from the original subplots of the experiment but from three 5 m. strips in each subplot arranged so that the central strip included the drain. For drain III the results were, in kantars per feddan:

South strip 5.37, central strip 6.00, north strip 5.63. The other comparisons showed no superiority in the central strip.

Other yields were as in Table XXI, none of the treatment differences being significant.

Table XXI.

	Drained	Undrained	Average
N only (=control)	5.34	5.47	5.41
NP	5.48	5.35	5.42
NK	5.59	5.64	5.62
NPK	5.17	5.70	5.44
Belt strips (no nitrogen)			3.74

N = Ammonium sulphate, 300 lb./acre.

P = superphosphate, 120.0 lb./acre.

K = potassium sulphate, 600 lb./acre.

Since the lateral action of a drain is narrow the drain serves only a part of the plot in which it lies, and direct comparison of effluent with amount of water applied is misleading. For example, the subplots of the experiment described in section C above received about 10 m.³ water/day. If the subplots had been twice as wide, that is. 20 m. instead of 10 m., they would have required twice as much water, and it may be supposed that the amount of effluent would have been unchanged. It is

perhaps better to consider the results in relation to the length of drain. With continued watering the subsurface drains of brick and sand yielded about 4–5 m.³ effluent/day/20 m. length of drain. In plot 124, drain II, which gave the largest effluents, had a maximum flow of about 4–5 m.³/day/70 m. length of drain. It may be concluded therefore that the best of the drains in plot 124 underlying 30–9=21 in. of soil was about one-third or one-fourth as efficient as the brick plus sand drains underlying 6 in. of soil.

Water lay in the furrows of plot 124 long enough to make this a fair, if approximate, comparison. For example, the observations in Table XXII were made in the case of drain II during the period 1–7 February 1936.

Table XXII.

	Effluent in m. ³	
	Day	Night
Feb. 1st. Part watered	Nil	Nil
2nd. Fully watered	Nil	Nil
3rd. Furrows full	2.1	2.3
4th. Furrows full	2.0	1.3
5th. Furrows full	1.0	0.6
6th. Furrows one-quarter full	0.3	0.3
7th. No standing water	Nil	Nil

It should be noted that in ordinary field experiments different parts of a plot do not receive equal amounts of water, nor are successive waterings of a single small area exactly alike. In this instance the area served by drain II received a rather heavy watering, but the observations are fairly representative.

It is probable that these drains would have given less trouble if a thin layer of coarse sand had been put over the bricks.

III. THE USE OF SALTBUSHES

Discussing the use of saltbushes for soil reclamation Hilgard (1906a) stated that "since some of the saltbushes take up nearly one-fifth of their dry weight of ash ingredients, largely common salt, the complete removal from the land of a five ton crop of saltbush hay will take away nearly a ton of alkali salts per acre".

In season 1934–5 Queensland saltbush (*Atriplex Muelleri*) grown at the Gezira Research Farm gave a yield of 4 tons of dry material per acre and was found to contain a high percentage of sodium. Further analyses were made in the following season and are presented below. It appears that the growing of saltbushes is not to be recommended as a means of

removing from soil such large amounts of salt as are involved in soil reclamation. For removing the relatively small amounts of salt introduced by irrigation water and so preventing deterioration of the soil saltbushes may, however, prove invaluable.

Analysis of Queensland saltbush

In season 1935-6 Queensland saltbush (*Atriplex Muelleri*) was grown on land which had been treated in 1927 with gypsum (2.00 tons/acre), potassium sulphate (2.02 tons) and sodium sulphate (3.74 tons) respectively. There was poor agreement in growth on replicate plots, and it appeared that the experiment was upset by interference from tree roots and other factors. The analyses of saltbush showed no relation to treatment and accordingly are reported as averages in Table XXIII as percentages of the dry matter.

Table XXIII. *Queensland saltbush, plot 52*

	Ca	Mg	Na	K	N	P ₂ O ₅	S	Cl	Cl/Na	Dry wt. as percentage of total crop
Leaves	1.25	0.61	10.54	1.39	3.74	0.68	0.81	7.18	0.68	31
Stems	1.23	0.28	5.85	0.70	1.71	0.43	0.38	6.08	1.04	31
Seed	0.83	0.29	4.28	1.27	1.93	0.53	0.36	4.85	1.11	38

Further data were obtained from material grown in another experiment. In season 1934-5 Queensland saltbush (*Atriplex Muelleri*) had been grown on plot 8 by the Plant Pathologist on land which had borne eight crops of continuous cotton; a good yield of 3.8 tons of dry material per acre was obtained. In the following season half of the subplots had a second crop of saltbush, and there were comparison subplots of saltbush growing after cotton in the previous season. Growth of the "continuous" saltbush was markedly poorer. Analytical results, the

Table XXIV. *Analytical data for Queensland saltbush, plot 8*

	Leaves		Stems		Seed	
	C-S	S-S	C-S	S-S	C-S	S-S
Ca	0.97	0.90	1.51	1.02	0.77	0.57
Mg	0.47	0.50	0.22	0.18	0.31	0.27
Na	9.36	8.53	5.33	3.10	5.23	3.69
K	1.67	2.43	0.89	1.02	1.41	1.53
N	3.54	1.76	1.40	0.71	2.04	1.01
P ₂ O ₅	0.57	0.57	0.34	0.62	0.55	0.43
S	0.74	0.79	0.34	0.27	0.44	0.38
Cl	7.44	7.72	6.03	3.55	6.57	4.70
Na/K	5.6	3.5	6.0	3.0	3.7	2.4
Cl/Na	0.79	0.90	1.13	1.15	1.26	1.28
Dry wt. as percentage of total crop	39	30	29	28	32	42

C-S=saltbush after cotton.

S-S=saltbush after saltbush.

mean of two sets of analyses, are given in Table XXIV as percentages on oven-dry material.

The following points can be noted:

(a) The *very high* percentage of *sodium*, i.e. of a base which has a bad effect on the physical properties of soil.

(b) The greatly decreased *nitrogen* in the saltbush growing after saltbush, as was evidenced in the field by much poorer growth. It is obvious that saltbush if grown regularly must be included in a mixed rotation or must be manured.

(c) More *sodium* and less *potassium* are taken out by the better growing saltbush. This tendency is of obvious importance since the supply of potassium in the soil must be conserved.

(d) In spite of the high percentage of *chloride* it is noteworthy that a large proportion of sodium in the leaves is not in the form of sodium chloride (which has a Cl/Na ratio of 1.54).

(e) From the dry weights it is seen that the saltbush after saltbush was rather more mature owing to lack of nitrogen. In both cases the proportion of seed (ripe and unripe) is extremely high; this indicates the importance of harvesting before the seeds begin to fall.

Comparison of four varieties of saltbush

In season 1935-6 the following varieties of saltbush were grown on plot 90 by the Agricultural Section:

(A) Vilmorin's "arroche d'Australie"—listed as *Atriplex semibaccata*, but more probably *A. hortensis* according to Massey. This is a tall annual spinach-like plant which grew well at Shambat near Khartoum but was disappointing at Wad Medani.

(B) *A. halimoides*, which grew well.

(C) *A. semibaccata*, a prostrate plant which grew fairly well.

(D) Queensland saltbush (*A. Muelleri*), which grows as well as any.

Plant samples (N and S) were collected from the north and south halves of the experimental area and were separately analysed. The analyses were very similar, even in the case of varieties A and B which were at different stages of development, and accordingly mean results as percentages of the dry matter are given in Table XXV for each of the four varieties.

All varieties showed a high percentage of sodium, and it was satisfactory to find that *A. halimoides* and *A. Muelleri*, which grew best, were as efficacious as any in removing sodium and that they did not consume an unduly high proportion of potassium. The seed constituted

a large part of the plant in three varieties and especially in *A. Muelleri*. This again points to the need for early harvesting if Hilgard's stipulation of "complete removal" of the crop is to be met. The increase in chloride-sodium ratio in passing from leaves to stem and from stem to seed is noteworthy. Vilmorin's saltbush contained relatively little chlorine, and it may be conjectured that the roots of this variety failed to reach the chloride present in the subsoil; it is significant that this variety has not been grown successfully here.

Table XXV. *Saltbush varieties*

Variety ...	Leaves				Stems				Se		
	A	B	C	D	A	B	C	D	A	B	D
Ca	0.92	0.93	1.17	1.53	0.33	1.01	0.69	1.19	0.46	0.68	0.70
Mg	1.45	1.17	0.95	0.65	0.33	0.30	0.28	0.22	0.67	0.64	0.27
Na	6.71	8.86	8.16	9.24	3.12	4.38	4.34	4.12	4.09	6.38	3.47
K	1.36	1.87	1.49	1.13	1.03	1.36	0.93	0.60	1.67	2.13	0.92
N	4.12	3.32	3.46	3.17	1.43	1.21	1.79	1.06	4.49	2.53	1.50
P ₂ O ₅	0.73	0.47	0.57	0.46	0.36	0.26	0.36	0.25	1.04	0.50	0.34
S	0.83	0.57	0.49	0.63	0.37	0.38	0.40	0.31	0.75	0.50	0.35
Cl	2.78	9.62	8.88	8.57	2.17	5.39	5.09	5.07	3.27	8.40	4.37
Cl/Na	0.41	1.08	1.09	0.93	0.70	1.23	1.17	1.23	0.80	1.32	1.26
Na/K	4.9	4.7	5.5	8.2	3.0	3.2	4.7	6.9	2.4	3.0	3.8

Dry wt. as percentage of whole:

Sample N	41	45	56	23	54	43	43	26	5*	12	51
Sample S	15	37	55	24	50	37	44	29	35	26	47

* Seeds from north half were not analysed.

Hilgard (1906*b*) quotes an analysis for *A. semibaccata*. Calculated on a like basis the comparisons are:

Table XXVI.

	Gezira	Hilgard		Gezira	Hilgard
Ca	0.96	0.81	S	0.48	0.20
Mg	0.65	0.37	P ₂ O ₅	0.45	0.54
Na	6.48	5.10	Cl	7.21	4.71
K	1.24	1.83	Cl/Na	1.11	0.92

Summary of Queensland saltbush analyses

Table XXVII presents an averaged summary of the analyses for Queensland saltbush detailed above.

Table XXVII.

	Ca	Mg	Na	K	N	P ₂ O ₅	S	Cl	Cl/Na	Dry wt. as percentage of total crop
Leaves	1.25	0.58	9.71	1.40	3.48	0.57	0.73	7.73	0.79	31
Stems	1.31	0.24	5.10	0.73	1.39	0.34	0.34	5.73	1.12	29
Seed	0.77	0.29	4.33	1.20	1.82	0.47	0.38	5.26	1.21	40
Whole*	1.08	0.37	6.22	1.13	2.21	0.46	0.48	6.16	0.99	100

* By calculation from parts.

The effect on Gezira soil of growing and carting away a crop of saltbush

It is now possible to examine, in respect to the more important plant foods, the net effect on Gezira soil of raising and removing a crop of saltbush. The data are given in Table XXVIII.

Table XXVIII. *Lb. per acre of constituents in saltbush, cotton, irrigation water and soil*

	Removed by		Added by		Soil and water-soluble bases, etc.,			
	4 ton	3½ kantars	irrigation water		cumulative totals to a depth of			
	crop of saltbush	crop of cotton	3000 tons	6000 tons	1 ft.	2 ft.	3 ft.	4 ft.
Ca	97	Small	157	315	32300	60300	85400	—
Mg	33	Small	34	69	3100	4140	6200	—
Na	557	Small	65	130	4880	17600	32200	—
K	101	8	13	26	1660	4970	7450	—
N	198	60	3	6	1030	1990	—	—
P ₂ O ₅	41	2	—	—	5670	—	—	—
S	43	—	16	31	—	11	970*	2040*
Cl	552	—	16	32	110	272	640	1610

* No allowance for gypsum.

Note on Table XXVIII

Cotton.

An average crop of 3½ kantars seed cotton, Afifi variety, was found (Sudan Gov. Chemist, 1920, 1931) to contain 60 lb. N, 73 lb. K, and 25 lb. P₂O₅. As the lint and seed only are removed from the field and the rest of the plant burnt, the loss of K and of P₂O₅ is reduced to that in the lint (368 lb.) and seed (735 lb.), viz. 8 and 2 lb. respectively. Data for the other constituents are not available except for isolated samples of leaves (B); it is clear that the loss of Ca, Mg and particularly Na in the seed and lint must be small relative to the quantities applied in the irrigation water.

Irrigation water.

(1) The average analysis of Barakat III canal water from October to March (see § IV) is used, with figures of Beam for chloride and potassium. The figure for nitrogen is approximate only, from analyses of Beam.

(2) The water applied to cotton in a season is about 6000 cubic metres or tons; for a quick crop of saltbush this figure would be less, perhaps half.

Soil bases, etc.

(1) The data are given in cumulative totals 1st foot from data due to Cox; 2 ft. due to Vageler. & Cox; 3 ft. due to Vageler.

(2) For Ca, Mg, Na and K the figures refer to replaceable and water-soluble material only; calcium and magnesium need no further examination but for sodium and potassium further relevant data are as follows:

Potassium (K) acid soluble, 1st foot (Beam, 1911): 13,000 lb./acre.

Potassium (K) insoluble, 1st foot (Beam, 1911): 17,900 lb./acre.

Potassium (K) in clay after mild acid treatment (Joseph & Hancock, 1924): 9500 lb./acre.

Sodium (Na) in clay after mild acid treatment (Joseph & Hancock, 1924): 14,500 lb./acre.

(3) Nitrogen is calculated on the basis of 290 p.p.m. in 1st foot, and 270 p.p.m. in 2nd foot. This is *total* nitrogen.

(4) Phosphorus (as P_2O_5), acid soluble (Beam, 1911), averages about 0.16% on 1st foot soil, i.e. about 5670 lb./acre. Vageler & Alten (1932) give data indicating a variation from 0.10 to 0.15% in the first 6 ft.

(5) Sulphur (as SO_4) is more or less absent in the first 2 ft. of soil, below which it occurs in large quantity. The data quoted (Joseph, 1925) do not allow for gypsum in 3rd and 4th feet.

(6) Chloride increases in quantity with depth and only becomes at all important from the beginning of the grey, relatively impervious, subsoil. The figures given are means of a recent analysis and of those quoted by Joseph (1925).

The most striking feature of the saltbush analyses is the removal of sodium. It will be seen, however, that to reduce the exchangeable and water-soluble sodium of the first 3 ft. of soil to half the present value would require about thirty-five crops of saltbush, each crop being reckoned as 4 tons dry material. On the other hand, to eliminate the sodium added in the irrigation water during a cotton season would require, on the same basis, about one-quarter of a saltbush crop. The present rotation in most of the Gezira is cotton-fallow-sorghum-fallow or leguminous crop-fallow-cotton-fallow-fallow. In 8 years the land thus carries two crops of cotton and one of sorghum, with some leguminous crop (*Dolichos lablab*). The amounts of water used by the grain and leguminous crops are roughly half that required for cotton, and it may be concluded therefore that with this rotation *one crop of saltbush every 12-13 years should be sufficient to remove all added sodium*, provided, of course, that the saltbush crop is harvested before seed-fall and is completely removed from the land. The potentialities of this crop for upkeep of soil fertility are not lightly to be disregarded.¹ That evidence of soil deterioration has not yet been found does not mean that it is not occurring, albeit at an extremely slow rate. A simple comparison could be made from Table XXVIII to indicate the slowness of accumulation of sodium in the soil from irrigation water; whether the results would be unduly optimistic or pessimistic as regards soil deterioration we are not yet in a position to say.

¹ It appears that the deep-rooting habit of saltbush produces a temporary physical modification in the soil. In recent field observations Clouston (1935-6) and Portsmouth (1936-7) found that cracks in a saltbush plot, 6 weeks after its last watering, were traced to a depth of 69 in. against 39 in. only in a comparable cotton plot. Roots of saltbush have been traced to a depth of 90 in. It was found also that the number of standard impacts required to drive a pointed iron rod into fallow soil was less in plots which had grown saltbush than in those which had grown cotton. There was markedly less resistance to penetration in the fifth 6 in. step of the former with little or no difference above. The result is best explained by the opening up of the soil by the extensive root system of saltbush.

Further study of the data in Table XXVIII shows that a considerable amount of potassium is removed from the soil by saltbush. The amount in the soil, however, is relatively large, especially if acid-soluble material is taken into account. No indication of potassium deficiency has been obtained in this area in spite of the contrary opinion expressed by Vageler & Alten (1932). Repeated cropping with saltbush might, however, render advisable an application of potassium. The amount of potassium removed in the seed and lint of an average ($3\frac{1}{2}$ kantar) cotton crop has been estimated (Sudan Govt. Chemist, 1920, 1931) at about 8 lb./acre, so that there may be a slight accumulation of this element during the course of a cotton season.

Consumption of phosphorus by saltbush is not excessive in comparison with reserves present in the soil but exceeds the modest 2 lb./acre of pentoxide removed in the seed and lint of an average cotton crop. Little is known as to the availability of soil phosphorus, but it may be mentioned that the negligible results of manuring with superphosphate and with potassium sulphate reported in Table XXI above confirm those of numerous earlier trials.

Nitrogen consumption by saltbush is about three times that of an average cotton crop; regeneration of supplies in the soil is normally possible by use of a suitable rotation of crops.

The data for chlorine are of interest. Removal by saltbush is on an extensive scale; supplies are small in the upper soil and are not large in the saline subsoil where the element tends to accumulate. Irrigation water does not add much. In fact, in the first 4 ft. of soil there appears to be sufficient chlorine for three or four crops only of saltbush. To obtain supplies the plant roots must descend well into the grey subsoil; ability to thrive will presumably depend on ability of plant roots to grow healthily in this layer. This may explain certain field results for growth of cotton following saltbush, which appeared better than that of cotton following one year's fallow. The effect, if genuine, can hardly be ascribed to the removal of sodium from the soil by a single crop of saltbush but may show a beneficial opening up of the subsoil by deep root penetration and subsequent drying out. It will be of great interest to test the effect of treatment with chlorides, e.g. calcium chloride.

IV. ANALYSES OF IRRIGATION WATER

The work on drainage and on saltbushes described in previous sections demanded a knowledge of the dissolved salts in the Blue Nile water used for irrigation. We are fortunate in possessing a series of analyses of water collected in the years 1905-7 at Khartoum by Beam (1906, 1908). The figures show some wide variations which are not easily correlated with seasonal flow, and since accurate sodium estimations are now conveniently obtained by the magnesium uranyl acetate method it seemed of interest to repeat the analyses and extend them to provide a comparison of Blue Nile water with that reaching the Research Farm after passage through 60 miles of canal. Accordingly, weekly samples were collected over a period of 11 months from (a) the Barakat III canal serving the Research Farm near Medani, (b) the river at Medani (some 150 miles upstream of Khartoum). For the collection of the latter samples we are indebted to Mr T. G. Pope.

Analysis has been confined to calcium, magnesium, sodium and sulphate ions (given in parts per million in Tables XXIX and XXX) and alkalinity (expressed as ml. of 0.1 N HCl required for titration of 100 ml. of water).

Table XXIX. *Monthly comparison of river and canal waters*

Date	Blue Nile						Barakat III canal						River gauge
	Ca	Mg	Na	SO ₄	Alk.	Ca/Na	Ca	Mg	Na	SO ₄	Alk.	Ca/Na	
1936													
May	31.0	7.2	11.6	16.4	2.29	2.67	30.0	7.6	16.2	17.6	2.33	1.85	10.3
June	24.3	6.0	9.8	13.3	1.73	2.49	30.8	7.0	16.0	18.3	2.35	1.92	11.1
July	21.5	4.8	5.5	8.8	1.38	3.91	28.3	5.5	13.0	13.0	2.01	2.17	15.5
Aug.	25.4	5.0	6.4	10.0	1.45	3.97	24.4	5.0	10.6	12.2	1.71	2.30	18.7
Sept.	22.0	5.0	6.0	6.8	1.34	3.58	18.3	3.8	23.5	8.8	1.79	0.78	18.9
Oct.	19.6	4.6	8.4	5.6	1.41	2.33	22.4	4.8	10.0	6.0	1.57	2.24	15.4
Nov.	20.5	4.8	8.5	5.5	1.49	2.41	22.3	5.3	9.8	5.8	1.60	2.28	12.3
Dec.	21.0	5.0	8.0	6.3	1.51	2.63	22.3	5.0	8.5	6.3	1.59	2.62	11.2
1937													
Jan.	22.8	5.0	9.0	6.6	1.75	2.53	23.4	4.8	9.0	8.8	1.69	2.60	10.3
Feb.	24.5	4.8	8.8	6.8	1.79	2.80	24.5	4.8	9.8	7.3	1.85	2.51	10.0
Mar.	25.0	6.0	10.6	7.6	1.95	2.36	25.2	6.0	11.0	7.6	1.95	2.36	10.0

River gauge—readings at Wad Medani by Irrigation Department (in metres).

It was satisfactory to find close agreement between the recent data and those recorded by Beam 30 years ago. The important calcium/sodium ratio is accurately determined. The analyses of river water show a seasonal variation bound up with the summer flood. During September, when irrigation is greatly reduced, abnormal values were obtained for

Table XXX. *River and canal waters—Summary*

	Ca	Mg	Na	K	SO ₄	Cl	Alk.	SiO ₂	Ca/Na
1904-7, Boam (18-29 analyses per component)	20.2	7.1	7.5	2.0	6.3	2.4	1.66	19.5	2.69
1936-7, River:									
May-March	23.4	5.3	8.4	—	8.5	—	1.64	—	2.88
October-March	22.2	5.0	8.9	—	6.4	—	1.65	—	2.51
1936-7, Canal:									
May-March*	25.4	5.4	11.4	—	10.3	—	1.87	—	2.29
October-March	23.4	5.1	9.7	—	7.0	—	1.71	—	2.44
Minor watering channel:									
November-March†	24.6	4.6	11.9	—	8.6	—	1.70	—	2.07

* Excluding September.

† Mean of nine analyses of water entering drainage plot about $\frac{1}{2}$ mile from canal; taken in November to March.

canal water which had presumably changed during its slow passage from the dam. During the main irrigation period of October to March, however, differences between river and canal water were small, the calcium/sodium ratio in the latter being rather lower as would be expected. Passage of water along a minor watering channel was found to produce a further change of the same kind.

SUMMARY AND CONCLUSIONS

After reviewing the possibility of soil deterioration in the Gezira and its dependence on change in the exchangeable bases in the soil we have given an account of field trials with soil improvers. Increased penetration of water, improved supply of nitrogen and higher yields were obtained, but the effects were not lasting. A part of the initial response is ascribed to the flocculating action of salts formed near the soil surface by interaction between soil and soil improver. With continued watering these salts are washed from the surface soil, but the applications of soil improver were insufficiently heavy and the leaching insufficiently thorough to effect any deep-seated change in the soil. Drainage experiments in which effluents were measured and analysed showed small changes in the right direction, but their main outcome has been strikingly to confirm the view that lateral movement of water through Gezira soil is so slight as to promise small hope of achieving any large-scale improvements by means of subsoil drainage. Analyses of saltbush have been made and showed that although these plants remove much sodium from the soil they can hardly be regarded as a practicable agent in soil improvement, since the amount of sodium in the soil is comparatively large. On the other hand, it appears that by including saltbush in

rotation and by removing the crop from the land it is possible to guarantee that no progressive deterioration will occur in consequence of accumulation of sodium introduced in the irrigation water. Further analyses of irrigation water were made in this connexion and substantially confirmed Beam's earlier data.

We do not yet know whether, under normal irrigation, the general tendency is for an accumulation of sodium or whether, on the contrary, salts are slowly being washed from the soil column (Greene & Peto, 1934). Until the nature and extent of chemical changes in the soil are accurately assessed it is impossible to say what annual expenditure on soil improvers, drainage, growing and disposal of saltbush is needed for maintenance of soil fertility. Further laboratory work should be directed to the detailed study of base exchange in Gezira soil and to observation of the physical characters on which permeability depends while, in the field, further experiments should be made in the use of soil improvers and drainage; information should also be sought as to the most convenient and least expensive way of including saltbush in the rotations best suited to different parts of the Gezira and as to the economic disposal of saltbush ash.

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EXPERIMENTAL METHODS WITH COTTON

1. THE DESIGN OF PLOTS FOR VARIETY TRIALS

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(With Two Text-figures)

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INTRODUCTION

AN important aspect of the work of the Plant Breeding Section of the Cotton Experiment Station at Barberton is the testing out each year of promising new strains and re-selections against older and better known strains. Every year seven or eight variety trials are laid down on the Station alone, while additional trials are frequently carried out on neighbouring farms.

Good planting conditions generally last a very few days at a time and may not recur for long intervals. It is very necessary, therefore, that the planting of these trials should be carried out as rapidly as possible when the opportunity occurs. Experience has shown that randomized block experiments, using long and narrow plots, can be planted very quickly

and accurately, and the necessary strict supervision is comparatively easy. The plots previously used have been two or four rows in width by about eighty to ninety feet in length. The present experiment was designed to give information on the comparative accuracy of various sizes and shapes of plots of this general type. A further point of interest was the effect on accuracy of including a smaller or larger number of strains in one experiment.

MATERIAL

Uniformity trials were carried out at Barberton on two fields in the season 1935-6 and on one field in the season 1936-7.

The Experiment Station is laid out in a series of rectangular fields, each being 560 ft. long, the width varying from 168 to 190 ft. In each field the area used for the uniformity trial was 144 rows of 4 units in length, making a total of 576 single row plots, each one unit long. The length of unit varied slightly, being 30 ft. on one field and 40 ft. on the other in 1935, and 36 ft. in 1936. Ample guard rows were allowed around the experimental area.

Planting was done by hand, the rows being 3 ft. 6 in. apart, with a spacing of 2 ft. between the plants in the row. This differs from the method of planting in the uniformity trial carried out by Hutchinson & Pause (1935) with cotton in India, where a measured quantity of seed per row was drilled in, the spacing between the plants in the row being irregular. Acid treated seed of O52, the U4 derivative which is at present in general cultivation in the Barberton district, was used on all three fields.

The two fields used in 1935-6 were both in rather a low state of fertility and the season was unfavourable for cotton. The extreme lateness of the rains delayed planting till late December, 6 weeks after what is generally considered to be the best time, and a drought in February seriously affected the already backward crop. Growth was poor and patchy and the very low yield of about 400 lb. seed cotton per acre was obtained from each field.

The field used in 1936-7 was in a better state of fertility and the season was much more favourable. Planting was carried out early in November, after good early rains, and the season's rainfall was heavier and better distributed than in the previous year. The crop grew well and was as uniform as is normally expected on the experimental area. Some of the early crop was taken by American bollworm (*Heliothis armigera* Hubn.), but the middle and top crop came away well and the average yield for the field was over 1100 lb. seed cotton per acre.

The whole experiment thus included results from two very different types of crop, poor and obviously patchy against good and apparently uniform, obtained under very different conditions. The results from the three fields agree closely in essential details regarding the relative accuracies of different shapes and sizes of plot and it is felt, therefore, that considerable reliance can be placed on the information obtained.

STATISTICAL ANALYSIS

(1) *Method employed*

The units were grouped to give plots 1, 2 and 4 rows wide and 1, 2 and 4 units long. The plots so formed were then grouped together to form blocks of 6, 9 and 12 plots in a row. No allowance was made for guard rows between plots when making these calculations, as the variety trials at Barberton are at present designed to test out U4 strains, which are now very much of one general type and show comparatively small differences in height, growth rate, etc. The analysis of variance method devised by Fisher (1930) was used throughout.

The result of the analysis of variance for 1 row plots, 1 unit (36 ft.) long, is given in Table I. The plots were grouped in blocks of 9 plots in a row.

Table I. *Analysis of variance of weight of seed cotton
in 1 row plots, 1 unit long*

	D.F.	Sum of squares	Variance	S.E.	% S.E. per plot
Between blocks	63	39892125.1	633208.3	—	—
Within blocks	512	21015288.9	41045.5	202.6	13.81
Total	575	60907414.0	105925.9	—	—

576 plots, grouped together in blocks of 9, give 64 replications, or 63 degrees of freedom for the variation between blocks. For the variation between plots within blocks there are 512 (8×64) degrees of freedom, making a total of 575 degrees of freedom for the 576 plots.

It will be observed that the removal of the variation between blocks has reduced the variance from 105925.9 to 41045.5, a reduction of 61.25%.

All the combinations of plots referred to above were analysed in this manner.

(2) *Percentage standard error per plot*

Table II gives the percentage standard error per plot for all three fields, taking 6, 9 and 12 plot blocks.

Table II. *Percentage standard error per plot*

Length in units	6 plots per block Width in rows			9 plots per block Width in rows			12 plots per block Width in rows		
	1	2	4	1	2	4	1	2	4
Field A, 1935-6; 1 unit = 30 ft.									
1	17.99	18.81	19.78	19.87	20.54	21.07	21.13	21.65	21.42
2	13.56	15.87	17.51	15.88	17.36	18.45	17.07	18.77	20.44
4	10.15	12.14	12.77	12.04	13.12	14.02	13.14	13.39	14.34
Field B, 1935-6; 1 unit = 40 ft.									
1	18.48	16.92	20.44	20.02	20.46	20.74	20.96	21.61	21.06
2	14.46	13.30	16.55	15.80	16.56	16.40	15.75	17.57	17.25
4	10.04	9.61	11.87	10.98	11.03	12.30	11.43	12.48	11.86
Field C, 1936-7; 1 unit = 36 ft.									
1	12.31	12.43	13.54	13.81	13.06	15.92	15.86	14.62	16.63
2	9.47	10.33	10.73	10.69	10.36	13.04	11.69	11.58	13.86
4	6.23	8.24	9.04	8.02	8.03	11.36	9.04	9.45	11.32

The most striking point about these figures is the very rapid fall in the standard error as the length of the plot is increased. This applies to all widths of plot. In some cases the reduction of the standard error due to lengthening the plot is almost as great as would be obtained by an equivalent number of repetitions of the shorter plot (see also Table IV).

When *plots of the same size* are compared the effect of lengthening the plot is still more marked and a fourfold lengthening and narrowing commonly reduces the standard error by approximately half. This is shown clearly if the table is read diagonally from the top right-hand to the bottom left-hand corner, for each block size for each field.

It will be seen that the standard error generally rises slightly, for plots of any given length, as the width is increased. This agrees with the results obtained by Kalamkar (1932) in his work on potatoes, but differs from the findings of Hutchinson & Panse (1935) working with cotton in India, and from the results of most other experiments in field plot technique, where any increase in plot size usually leads to a drop in the standard error.

The actual standard errors are much higher for fields A and B, for reasons already given, but, in spite of this, the general results are in strict accordance with those from Field C.

Comparing the different block sizes, it will be seen that the standard error rises steadily as the block size is increased by the addition of more plots. The figures were examined to see whether the size and shape of plot affected this rise in standard error due to larger block sizes. For all types of plot the standard error for 6 plot blocks was put at 100% and the corresponding figures were worked out for 9 plot and 12 plot blocks, thus

giving the percentage rise in the standard error for larger blocks. The figures were somewhat irregular but it was clear that length of plot did not affect the issue: on the other hand there was a tendency for the 4 row plots, of any length, to give a smaller rise in standard error than the 1 row plots when the block size was increased from 6 to 12 plots. This is brought out by the following mean figures.

Table III. *Relative standard errors, means for all lengths, Fields A, B and C*

	6 plots per block	9 plots per block	12 plots per block
1 row plots	100	112.9	122.9
2 row plots	100	110.0	119.7
4 row plots	100	110.1	113.5

These figures show more clearly than the actual standard errors of Table II that the loss of accuracy is very appreciable when the block size is increased. Thus for the 1 row plots the number of repetitions required for 12 plot blocks would be 50% greater than for 6 plot blocks. It is obviously desirable to keep the number of strains in a variety trial as low as possible. The most desirable number must vary according to circumstances, and some estimate of the effect of varying numbers of strains on the accuracy of a given type of plot is of considerable value as a guide in arranging for the testing of a large number of strains.

(3) *Number of replications and area of land required*

The calculations made for Table IV were based on a standard error of 4% of the mean, which means that differences of over 11% of the mean can be relied on as significant at $P=0.05$. A standard error of 4% is purely an arbitrary figure, chosen for convenience. The relative numbers of replications and areas of land required would remain the same for any degree of accuracy chosen.

In field A, with plots 4 rows wide \times 1 unit long an area of 2.42 acres is required, as against 0.87 acre, *for the same size of plot*, when the shape is altered to 1 row wide \times 4 units long. Corresponding figures in fields B and C are 3.11 acres compared with 0.92 acre, and 1.67 acres compared with 0.52 acre.

The high standard errors given by fields A and B are reflected in the large number of replications required as compared with field C, generally about twice as many. Fortunately a combination of such poor conditions does not often occur and the experimental material is more generally of about the standard of field C.

Table IV. *Number of replications and area of land required to give a standard error of 4% of the mean*

Length in units	Width in rows					
	1		2		4	
	No. of reps.*	Area (acres)	No. of reps.*	Area (acres)	No. of reps.*	Area (acres)
Field A, 1935-6; 1 unit = 30 ft.						
1	25	0.54	27	1.17	28	2.42
2	16	0.70	19	1.64	22	3.81
4	10	0.87	11	1.90	13	4.50
Field B, 1935-6; 1 unit = 40 ft.						
1	26	0.75	27	1.56	27	3.11
2	16	0.92	18	2.08	17	3.92
4	8	0.92	8	1.85	10	4.62
Field C, 1936-7; 1 unit = 36 ft.						
1	12	0.31	11	0.57	16	1.67
2	8	0.42	7	0.73	11	2.29
4	5	0.52	5	1.04	9	3.75

* Number of replications is always given to the nearest whole number above the amount actually required, area being based on this number.

(4) *Efficiency per unit area of land*

A convenient method of representing the relative values of different types of plot, in terms of land required, has been used by Kalamkar (1932) and Justesen (1932). A figure for "efficiency" is obtained which takes into account not only the standard error per plot, and hence the number of replications required for a given degree of accuracy, but also the size of plot and the area of land that will be required. In effect the relative efficiencies of various types of plot are inversely proportional to the areas required to give the same amount of information.

The efficiency can be found by multiplying the percentage variance per plot by the number of units used to make up the plot, and taking the reciprocal. Taking the highest efficiency (in the case of each field the 1 row and 1 unit plot) as 100%, the efficiency of the other plots may be based on this. Figures for all three fields, for 9 plot blocks only, are given in Table V.

The figures for these fields show a remarkable degree of similarity considering the differences in growth. Once again the superiority of long and narrow plots over shorter and wider ones is clearly brought out, particularly if Table V is read diagonally as advocated previously. In every case plots 4 units long \times 1 row wide are between three and four times as efficient as plots 1 unit long \times 4 rows wide.

Table V. *Efficiency of plots in use of land (9 plots per block)*

Length in units	Width in rows		
	1	2	4
Field A, 1935-6; 1 unit = 30 ft.			
1	100	47	22
2	78	33	15
4	68	29	13
Field B, 1935-6; 1 unit = 40 ft.			
1	100	49	23
2	80	37	19
4	83	41	17
Field C, 1936-7, 1 unit = 36 ft.			
1	100	56	19
2	83	44	14
4	74	37	9

The available information regarding the influence of size and shape of plot on efficiency is concisely tabulated in Table VI. The percentage standard errors per plot (Table II) are also included in this table for convenience in comparison.

Efficiency depends on the combination of two factors, size of plot and shape of plot. With plots of any given size, the efficiency rises as the plot shape becomes progressively longer and narrower: with plots of any

Table VI. *Influence of size and shape of plot on standard error and efficiency (9 plots per block)*

Field and year	Plot size acres	Plot shape		% S.E. per plot	Efficiency %
		Rows \times units	$W \times L$		
A 1935-6	1.207	1 \times 2	1:17	15.88	78
		2 \times 1	1:4	20.54	47
C 1936-7	1.173	1 \times 2	1:21	10.69	83
		2 \times 1	1:5	13.06	56
B 1935-6	1.156	1 \times 2	1:23	15.80	80
		2 \times 1	1:6	20.46	49
A 1935-6	1.104	1 \times 4	1:34	12.04	68
		2 \times 2	1:9	17.36	33
		4 \times 1	1:2	21.07	22
C 1936-7	1.86	1 \times 4	1:41	8.02	74
		2 \times 2	1:10	10.36	44
		4 \times 1	1:3	15.92	19
B 1935-6	1.78	1 \times 4	1:46	10.98	83
		2 \times 2	1:11	16.56	37
		4 \times 1	1:3	20.74	23
A 1935-6	1.52	2 \times 4	1:17	13.12	29
		4 \times 2	1:4	18.45	15
C 1936-7	1.43	2 \times 4	1:21	8.03	37
		4 \times 2	1:5	13.04	14
B 1935-6	1.39	2 \times 4	1:23	11.03	41
		4 \times 2	1:6	16.40	23

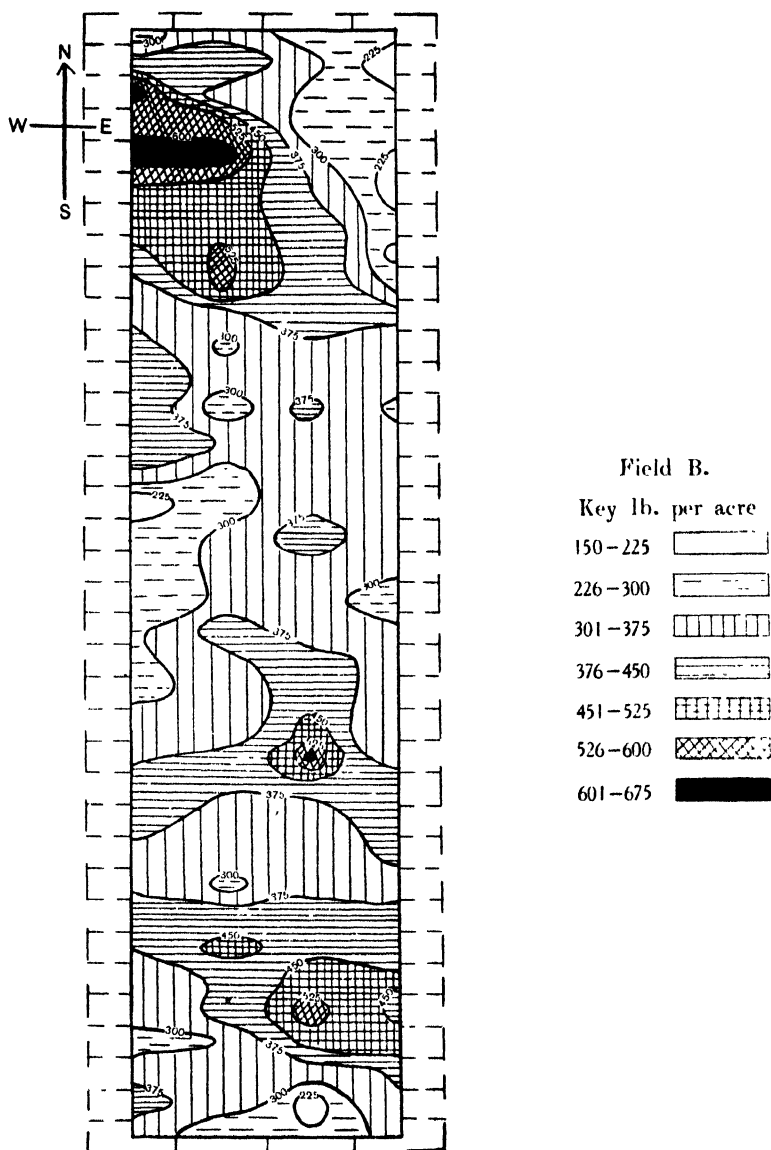


Fig. 1. Fertility contour map of Field B, showing yields in pounds per acre of seed cotton. The map is based on a plot size of 4 rows wide by 1 unit long. The actual size from which yields were obtained is shown by the outer broken line, the area mapped necessarily terminating at the centre of all outer plots.

given shape the efficiency rises as the plots become smaller. Thus a particularly long and narrow plot can have a higher efficiency than a plot only half its size, of a less suitable shape, as can be seen in Table VI by comparing the different sized plots on any particular field.

The very high efficiency of 1 row plots should be noted; they appear to be on the average nearly twice as efficient as 2 row plots, and they should prove very useful in experiments with closely allied strains, where seed and land are limited, and where the extra labour involved at planting and harvesting is immaterial.

(5) *Fertility contour maps*

Fertility contour maps for fields B and C are shown in Figs. 1 and 2. The maps are prepared direct from the yield data (lb. per acre) and not on a percentage basis as is customary; this was done in order to bring out the actual yield differences between the two fields. The yield figures were combined to form plots 4 rows wide \times 1 unit long, and the resulting data mapped in the usual way, assuming the average yield of each plot to be at its centre.

Correlations were calculated, for all three fields, from north to south and from east to west, and the results revealed that there was no general fertility gradient in either direction on field A and B; in the case of field C a slight gradient was found from east to west, chiefly on account of the low yield of the eastern series of plots.

The most striking feature of these maps is that the irregularity in yield shows up as a rather small-scale patchiness with little tendency to any regular fertility gradient. It was the common experience of this type of patchiness on the Station that led to the use of long narrow plots as a general practice from the beginning. There is little doubt that it is largely responsible for the very marked advantage of such plots as shown by this experiment. Contributing causes to this patchiness, in addition to soil heterogeneity, may be found in the stunting of the young plant by aphids (always found here in association with nests of the black ant, *E.C.G.C. Reports* (1937)), and destruction of crop by other pests.

DISCUSSION AND CONCLUSIONS

Full figures are given in the appendix, for each field, for size of plot, percentage standard error, number of replications and area of land required, taking 6, 9 and 12 plots per block. These tables are presented in the same manner as those given in the paper by Hutchinson & Panse (1935), and may be of interest to others experimenting with cotton.

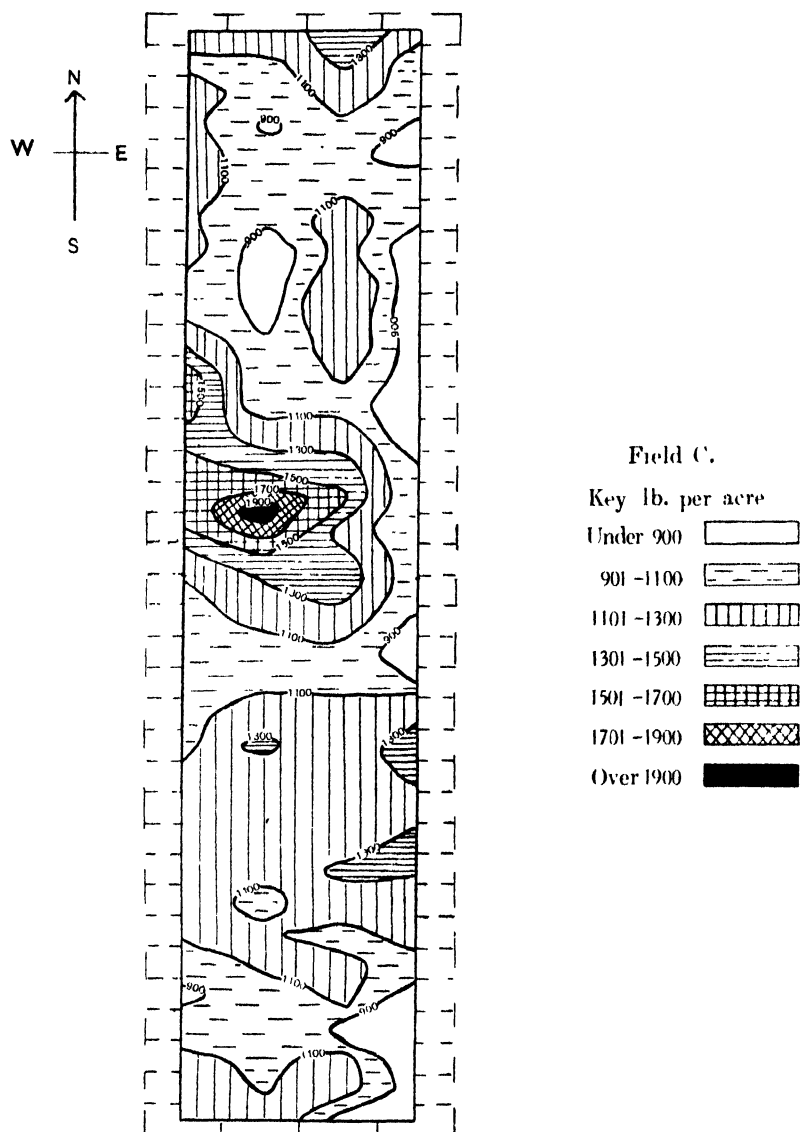


Fig. 2. Fertility contour map of Field C, showing yields in pounds per acre of seed cotton. The map is based on a plot size of 4 rows wide by 1 unit long. The actual field size from which yields were obtained is shown by the outer broken line, the area mapped necessarily terminating at the centre of all outer plots.

The nature of the experiment and matters of agricultural convenience will determine the size of plot to be used, but it should be borne in mind that small plots are more efficient than larger ones, and whatever the size of plot ultimately chosen it should be as long and narrow as possible.

These conclusions are in general agreement with the results of most other workers on field plot technique and plot shape, with cotton as well as with other crops; all of these reveal that long and narrow plots are preferable to shorter and wider ones.

In actual practice at Barberton long plots, of about 160 ft. in length by 2 rows wide, have now been adopted for ordinary variety trials in place of 2 row plots of about half that length. Although these plots, being double the size, have a slightly lower efficiency than those used previously, they are far more efficient than any other shaped plot of the same size that would fit the fields conveniently. By using these larger plots the number of repetitions required is considerably reduced and it is found that, in spite of the area occupied being slightly greater, planting can be carried out more quickly and labour is saved in other operations such as picking and weighing. Another point of importance is that close supervision in all the important operations is more easily carried out with a smaller number of longer plots.

One row plots have not been adopted here, in spite of their high efficiency, as it is considered that two row plots provide the minimum breadth requirement in trials where observations on the growth and development of the different strains are constantly being carried out. These observations and development studies always contribute appreciably to the information obtained from any trial. Further, one row plots would entail much greater supervision at planting and picking, and the risk of mixing strains would be far greater.

The necessity for simplifying the experimental layout, when working with African labour, is of vital importance, and some idea of the difficulties encountered at Barberton in this connexion is given by Fielding (1936).

SUMMARY

1. The results of three uniformity trials with a U 4 cotton at Barberton are reported. Two of these trials, carried out in a dry year, gave yields in the region of 400 lb. seed cotton per acre; the third, in a wet year, yielded over 1100 lb. per acre.

2. Results from the three experiments agreed closely in essential details regarding size and shape of plots.

3. In all three cases the percentage standard error per plot decreased rapidly as the plot was lengthened, but tended to increase slightly as the width of the plot was increased.

4. The standard error increased as the block size was increased by the addition of more plots, indicating the desirability of keeping the number of strains in a variety trial as low as possible.

5. With plots of the same shape the smallest plots were the most efficient, while with plots of the same size the efficiency increased as the plot shape became longer and narrower.

6. Two fertility contour maps are given, which illustrate a general patchiness in yield common to cotton crops in the Barberton district.

7. Details of the types of plot used at Barberton are given, together with the reasons for their adoption.

ACKNOWLEDGEMENT

The authors wish to express their indebtedness to Mr F. R. Parnell, under whose general direction this work has been carried out, and whose advice and criticism throughout have been invaluable.

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APPENDIX

UNIFORMITY TRIAL, FIELD A, 1935-6

Number of replications and area of land required to give a standard error of 4% of the mean with different plot sizes and shapes

Plot size acres	Plot shape		6 plot blocks			9 plot blocks			12 plot blocks		
	Rows × units	B × L	% s.e.	No. of reps.	Acres	% s.e.	No. of reps.	Acres	% s.e.	No. of reps.	Acres
1/26	4 × 1	14 ft. × 120 ft.	12.77	11	2.54	14.02	13	4.50	14.34	13	6.00
1/52	4 × 2	14 ft. × 60 ft.	17.51	20	2.31	18.45	22	3.81	20.44	27	6.23
1/104	4 × 1	14 ft. × 30 ft.	19.78	25	1.44	21.07	28	2.42	21.42	29	3.34
1/52	2 × 4	7 ft. × 120 ft.	12.14	10	1.15	13.12	11	1.90	13.39	12	2.77
1/104	2 × 2	7 ft. × 60 ft.	15.87	16	0.93	17.36	19	1.64	18.77	22	2.46
1/207	2 × 1	7 ft. × 30 ft.	18.81	23	0.67	20.54	27	1.17	21.65	30	1.74
1/104	1 × 4	3 ft. 6 in. × 120 ft.	10.15	7	0.40	12.04	10	0.87	13.14	11	1.27
1/207	1 × 2	3 ft. 6 in. × 60 ft.	13.56	12	0.35	15.88	16	0.70	17.07	19	1.10
1/414	1 × 1	3 ft. 6 in. × 30 ft.	17.99	21	0.30	19.87	25	0.54	21.13	28	0.81

UNIFORMITY TRIAL, FIELD B, 1935-6

Number of replications and area of land required to give a standard error of 4% of the mean with different plot sizes and shapes

Plot size acres	Plot shape		6 plot blocks			9 plot blocks			12 plot blocks		
	Rows × units	B × L	% s.e.	No. of reps.	Acres	% s.e.	No. of reps.	Acres	% s.e.	No. of reps.	Acres
1/20	4 × 1	14 ft. × 160 ft.	11.87	9	2.77	12.30	10	4.62	11.86	9	5.54
1/39	4 × 2	14 ft. × 80 ft.	16.55	18	2.77	16.40	17	3.92	17.25	19	5.85
1/78	4 × 1	14 ft. × 40 ft.	20.44	27	2.08	20.74	27	3.11	21.06	28	4.31
1/39	2 × 1	7 ft. × 160 ft.	9.61	6	0.92	11.03	8	1.85	12.48	10	3.08
1/78	2 × 2	7 ft. × 80 ft.	13.30	11	0.85	16.56	18	2.08	17.57	20	3.08
1/156	2 × 1	7 ft. × 40 ft.	16.92	18	0.69	20.46	27	1.56	21.61	30	2.31
1/78	1 × 4	3 ft. 6 in. × 160 ft.	10.04	7	0.54	10.98	8	0.92	11.43	9	1.38
1/156	1 × 2	3 ft. 6 in. × 80 ft.	14.46	14	0.54	15.80	16	0.92	15.75	16	1.23
1/312	1 × 1	3 ft. 6 in. × 40 ft.	18.18	22	0.42	20.02	26	0.75	20.96	28	1.08

UNIFORMITY TRIAL, FIELD C, 1936-7

Number of replications and area of land required to give a standard error of 4% of the mean with different plot sizes and shapes

Plot size acres	Plot shape		6 plot blocks			9 plot blocks			12 plot blocks		
	Rows × units	B × L	% s.e.	No. of reps.	Acres	% s.e.	No. of reps.	Acres	% s.e.	No. of reps.	Acres
1/22	4 × 4	14 ft. × 144 ft.	9.04	6	1.67	11.36	9	3.75	11.32	9	5.00
1/43	4 × 2	14 ft. × 72 ft.	10.73	8	1.11	13.04	11	2.29	13.06	13	3.61
1/86	4 × 1	14 ft. × 36 ft.	13.54	12	0.83	15.92	16	1.67	16.63	18	2.50
1/43	2 × 4	7 ft. × 144 ft.	8.24	5	0.69	8.03	5	1.04	9.45	6	1.67
1/86	2 × 2	7 ft. × 72 ft.	10.33	7	0.49	10.36	7	0.73	11.58	9	1.25
1/173	2 × 1	7 ft. × 36 ft.	12.43	10	0.35	13.06	11	0.57	14.62	14	0.97
1/86	1 × 4	3 ft. 6 in. × 144 ft.	6.23	3	0.21	8.02	5	0.52	9.04	6	0.83
1/173	1 × 2	3 ft. 6 in. × 72 ft.	9.47	6	0.21	10.69	8	0.42	11.69	9	0.63
1/346	1 × 1	3 ft. 6 in. × 36 ft.	12.31	10	0.17	13.81	12	0.31	15.86	16	0.56

EXPERIMENTS ON THE SPACING OF SUGAR BEET

I. RESULTS BASED ON PLOT YIELDS

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(With One Text-figure)

SINCE sugar beet was first introduced into this country many experiments have been conducted to determine the effects of spacing on yield: the general advice based on these experiments is that beet should be spaced as closely as working conditions permit. Davies (1931) carried out a series of experiments in the West Midlands, and came to the conclusion that yield was not related to the number of roots per acre, but was affected by their distribution. His work demonstrated that wide row distances could not be compensated by narrow spacing in the row. He found that yield increased as row distance decreased down to 16 in., but that singling distances of 4-10 in. produced no differences in yield of roots: the yield of green leaves, on the other hand, was increased as singling distance decreased, but was unaffected by row distance (Davies & Dudley, 1929). Although Davies' results would be generally accepted as a true expression of the general rule, many isolated spacing experiments fail to conform to them; it is possible that discrepancies in results, that undoubtedly occur, may be due to variations in the "plant" actually obtained in the experiments. Engledow *et al.* (1928), as a result of counts and weights taken on ordinary farm crops of sugar beet, concluded that uniformity of "plant" was a most important spacing factor affecting yield. In America Brewbaker & Deming (1935) have found yield to be related to percentage stand (correlation coefficients varying from +0.35 to +0.70), the regression between the two variables being approximately linear over the range studied. They also found that uniformity of "plant" was more important than spacing distances, either between or in the rows. Their work showed that single gaps had little effect on yield, because neighbouring beet compensated for them to the extent of 96.2%; serious loss of yield only occurred, therefore, with adjacent gaps. Pedersen (1933) studied the relationship between

percentage of gaps and yield in a large number of Danish experiments with sugar beet and mangolds. In the case of sugar beet he found that the compensatory growth of neighbouring roots amounted to 76% for a single gap, and that the percentage compensation decreased as the size of gap (i.e. number of missing beet) increased. In an earlier paper (Pedersen, 1931) he had shown that under ordinary field conditions the distribution of gaps was approximately random.

Experiments were conducted in 1934 and 1936 on the Cambridge University Farm with the object of studying the effect of gaps under varying spacing conditions. These experiments involved very laborious field work, but the subsequent statistical work proved even more exacting; very considerable mathematical difficulties were encountered and it is hoped that further progress may be made in the future in surmounting these difficulties. The present paper describes only the experiments and the first statistical analyses which have been performed.

DESCRIPTION OF EXPERIMENTS

Both experiments were carried out on the same field, which consists of a light gravelly loam, the field being manured with farmyard manure and complete artificials. In each case there were five blocks, which were each divided into three main plots for distances between the row of 12, 18 and 24 in. In 1934 the main plot was divided into three for spacings within the row of 6, 9 and 12 in.; in 1936 the main plots were only two-thirds of the length they were in 1934, the 6 in. spacing in the row being omitted. Fig. 1 shows the lay-out for one block of the 1934 experiment with the discards that were allowed; in all cases the ultimate plot was precisely 8 by 4 yards, and the number of beet sites provided, together with the actual number of beet which survived, is shown in Table I.

Table I. *Possible and actual numbers of beet for the various spacings*

	12 × 6 in.	12 × 9 in.	12 × 12 in.	18 × 6 in.	18 × 9 in.	18 × 12 in.	24 × 6 in.	24 × 9 in.	24 × 12 in.
Possible no. beet:									
Per plot	576	384	288	384	256	192	288	192	144
Per acre	87,120	58,080	43,560	58,080	38,720	29,040	43,560	29,040	21,780
Actual no. beet:									
Per acre, 1934	61,075	40,202	32,095	40,081	25,107	21,145	29,736	19,693	15,760
Per acre, 1936	—	46,615	36,512	—	31,460	22,988	—	23,807	18,695

The following is a description of the 1934 experiment. The field was ploughed in the autumn, and lay in a winter furrow until late March

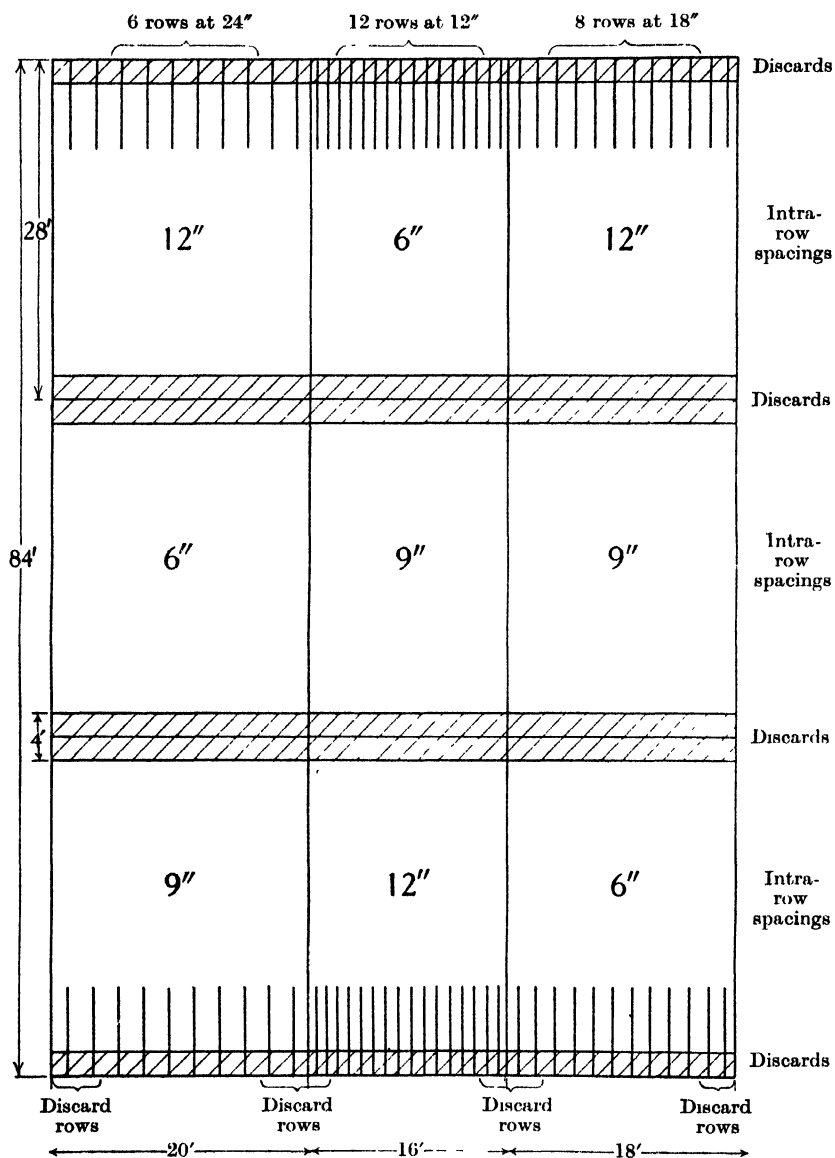


Fig. 1. Plan of one block of 1934 experiment.

when it was twice drag harrowed. On 11 and 12 April the conditions for sowing were good. The experimental area was rototilled and raked and strings were put down to mark the positions of the rows. Firmness was obtained by placing pliable planks along the strings and walking on them. The seed was dibbled by hand for the whole experiment, the variety used being Kleinwanzleben E. Holes for dibbling were made with irons carrying spikes at 3 in. intervals, and two seeds (i.e. fruits) were placed in every second, third or fourth hole, according to the spacing required; by starting the rows the same distance from the edge of the plot it was possible to ensure that the plants came up "on the square". Covering in was done with a light hand rake, care being taken not to disturb the seeds. The plots were hand hoed on 14 and 22 May, 5 June and 22 July and singled on 21 May. On 7 June the plots were mapped. For each plot a stiff card was used and ruled so that there was a square for each plant site; only the gaps were recorded at that stage. After the July hoeing the cards were checked, and it was found that practically no loss of plants had occurred in the interval, as was also found when the cards were checked immediately prior to the lifting of the beet in October.

The plots were harvested between 25 October and 12 November. The method was as follows:

(1) The plot card having been checked, beet were lifted with a fork, one row being taken out at a time, and the greatest care exercised to keep individuals in their proper order so that weights might be booked in the correct square on the card. On a few occasions there was a discrepancy (generally due to the presence of "doubles") between the number of beet in a row and the number shown on the card, and in these cases individual records were not kept; the loss of beet in this way, however, amounted to less than 3%, and the total weight of the beet concerned was, of course, included in the estimate of the total plot yield.

(2) The beet were carried to a temporary shelter close to the plots, where they were topped with a guillotine. In a few cases when topping was not quite accurate a little hand-saw was used to trim the top or the root.

(3) In view of the varying weather conditions that would be experienced, it was decided to dip each top into a tank of water, and then to give it a standardized shake before weighing it on a spring balance, which could be read accurately to 7 g.

(4) The root was washed in a tank, a hand scrubbing brush being used, and then was weighed on a machine to an accuracy of 1 g.

(5) One man was continuously employed recording, and he entered the weight of the top and of the root in the appropriate square on the plot card.

(6) Samples of the beet were taken for estimation of sugar percentage. In this connexion it is necessary to define a "perfect" beet as one which, when growing on the field, had no gap adjacent to it within the row, across the row or diagonally. The perfect beet formed one sample for sugar analysis for each plot, except when their number exceeded twenty-five, in which case twenty-five were drawn at random from amongst them. From the imperfect beet of each plot two random samples of twenty-five beet were taken; the method was to lay out the roots in a line and then, starting at random, to take every n th beet (n being the number present divided by 25).

The field labour involved was very great and amounted to nearly 1000 man hours. A group of seven workers was required at a time, and to ensure that accuracy was not lost through fatigue, 3 hr. relays were arranged.

The 1936 experiment was exactly similar to that of 1934, except that it was decided to omit the 6 in. spacing within the row; thus in 1936 each main plot was only divided into two sub-plots. The methods of working were exactly similar to those in the other experiment.

Very different weather was experienced in the two seasons 1934 and 1936. The following were the monthly rainfall figures:

	1934 in.	1936 in.
January	0.81	2.91
February	0.16	2.11
March	1.09	0.66
April	1.69	1.21
May	0.55	0.93
June	0.79	3.26
July	1.26	5.07
August	1.96	0.53
September	1.84	2.27
October	1.78	1.77

The year 1934 was extremely dry, and previous to August no month had a rainfall as large as the normal. On the other hand, January, February, June and July of 1936 had rainfall above normal. The great difference in rainfall was thus in the mid-summer period and the beet, particularly the closely spaced ones, in 1934 showed obvious signs of suffering from drought at this time, whereas in 1936 steady growth was maintained throughout.

In 1934 growth appeared quite uniform over the plots, but in 1936

some inequality was observable in summer; the sites of heaps of farmyard manure which had stood on the field in the previous autumn were discernible by the more luxuriant growth of the plants upon them, and this was responsible for rather higher errors in the second experiment.

RESULTS OF THE EXPERIMENTS. PLOT YIELDS

In each experiment the first statistical analysis was on the plot yields, obtained by adding the individual weights; the results are shown in Tables II and III for row widths and spacings within the row separately, since no interaction between these variables was significant. Yields of tops and yields of washed roots are both given, but yields of total plants have not been calculated as it is felt that the figures could have little meaning.

As regards weight of tops the only significant difference was obtained in 1934, when closer spacings within the row produced greater weights of tops; this is in conformity with Davies' finding. Distance in the row had no effect on yield of roots, but the narrower rows produced greater yields than the wider ones; the regression was highly significant in 1934 but insignificant in 1936, although the same general trend was observed. Despite the fact that deviations from linear regression were insignificant in 1934, in both years there was little difference between 12 and 18 in., but 24 in. gave lower yields of roots. In 1934 the narrow spacings, both in and between rows, gave sugar percentages that were higher than with the wider spacings, but in 1936 no differences were obtained in this respect. The regression, showing a decrease in yield of sugar with increasing row width, was very highly significant in 1934, but although the trend was the same in 1936 no significance was then obtained; spacing within the row had no effect on yield of sugar in either year.

Despite the greatest care some irregularity of plant is bound to occur in field experiments, and the method of covariance is a powerful statistical weapon for eliminating chance irregularities. Therefore the method has been used in both experiments to correct weight of tops, weight of roots and weight of sugar for variations in percentage plant. As regards weight of tops correction had little effect in 1934 on the comparison of row widths, but in 1936 it increased the figure for 18 in. rows, which then became higher than 12 and 24 in. The correction had no appreciable effect on the comparison of distances in the row. The figures for weight of roots for the three row widths were changed but little by the correction, but the reduction of error produced significance in 1936 where it had been lacking previously; in both cases corrected figures showed a

Table II. *Plot data for 1934*

	Distance between rows				Significance	Distance in rows				
	12 in.	18 in.	24 in.	S.E. of mean		6 in.	9 in.	12 in.	S.E. of mean	Significance
Percentage plant:										
Actual no. roots $\times 100$ Possible no. roots	70.99	68.92	69.24	2.686	Insig.	68.90	67.27	72.99	1.412	12 > 6, 9 in.*
Wt. tops (tons/acre)	8.81	9.29	9.06	0.241	Insig.	9.33	9.03	8.80	0.161	Regression*
Wt. washed roots (tons/acre)	13.80	13.73	13.01	1.403	Regression**	13.35	13.39	13.80	1.671	Insig.
Sugar percentage	18.27	17.88	17.93	0.181	12 > 18, 24 in.*	18.07	18.17	17.85	0.170	6, 9 > 12 in.*
Wt. sugar (tons/acre)	2.516	2.458	2.334	0.018	Regression***	2.411	2.431	2.465	0.033	Insig.
Wt. tops corrected for per- centage plant	8.87	9.26	9.04	0.223	Insig.	9.36	9.12	8.69	0.157	Regression*
Wt. roots corrected for percentage plant	13.84	13.70	12.99	0.106	Regression**	13.37	13.45	13.72	0.167	Insig.
Wt. sugar corrected for percentage plant	2.521	2.455	2.332	0.016	Regression***	2.415	2.441	2.453	0.033	Insig.
Wt. roots corrected for wt. tops	13.90	13.63	13.01	0.100	Regression***	13.16	13.40	13.97	0.132	Regression***
Wt. sugar corrected for wt. tops	2.527	2.447	2.333	0.015	Regression***	2.383	2.434	2.491	0.029	Regression*

* Significant with $P < 0.05$.

** Significant with $P < 0.01$.

*** Significant with $P < 0.001$.

Table III. *Plot data for 1936*

	Distance between rows				Distance in rows			
	12 in.	18 in.	24 in.	S.E. of mean	Significance	9 in.	12 in.	S.E. of mean
Percentage plant: $\frac{\text{Actual no. roots} \times 100}{\text{Possible no. roots}}$	82.04	80.20	83.72	1.163	Insig.	81.13	82.84	0.971
Wt. tops (tons/acre)	10.08	10.31	10.10	0.270	Insig.	10.15	10.17	0.344
Wt. washed roots (tons/acre)	17.88	17.26	16.62	0.396	Insig.	17.13	17.37	0.370
Sugar percentage	17.88	17.81	17.91	0.127	Insig.	17.91	17.83	0.084
Wt. sugar (tons/acre)	3.194	3.073	2.976	0.068	Insig.	3.067	3.096	0.060
Wt. tops corrected for percentage plant	10.07	10.62	9.79	0.189	18 > 12, 24 in.*	10.22	10.10	0.349
Wt. roots corrected for percentage plant	17.87	17.30	16.59	0.344	Regression*	17.27	17.24	0.343
Wt. sugar corrected for percentage plant	3.192	3.127	2.926	0.063	Regression*	3.093	3.071	0.057
Wt. roots corrected for wt. tops	17.98	17.08	16.70	0.213	Regression**	17.14	17.37	0.218
Wt. sugar corrected for wt. tops	3.210	3.045	2.990	0.041	Regression**	3.068	3.095	0.041

* Significance with $P < 0.05$.** Significance with $P < 0.01$.

significant linear decline in yield as row distance increased. Correction did not bring out any significant differences in yield of roots between different spaces within the row. Weight of sugar followed the same course as weight of roots.

Correction for weight of tops is also of some interest, as giving a comparative measure of the efficiency of the tops. The figures show that the tops were more efficient on narrower rows, this being highly significant in both years. In 1936 the efficiency of the tops for different spacings within the row showed no significant differences after correction, but in 1934 the efficiency was greater at the wider spacings. It thus appears that the maximum efficiency of the tops coincided with spacings of approximately 12 in. in each direction.

The average percentages of "plant" obtained in these experiments were approximately 70 and 80 respectively. These figures would be considered normal in practice, where care at singling can compensate for a somewhat gappy initial "plant"; in these experiments no compensation of that nature was possible.

In each year duplicate samples of twenty-five beet were taken from each plot (excluding the perfect beet) and the sampling errors for sugar percentage, based on 45 degrees of freedom in 1934 and 30 degrees of freedom in 1936, were calculated. The standard error for one determination was 0.433 in 1934 and 0.439 in 1936, these figures being 2.40 and 2.46 % of the mean sugar percentage respectively.

The practical conclusions from the experiments are:

(1) Although the yields of roots and sugar increase as the row distance decreases, there is little indication that rows narrower than 18 in. are economically worth while, as further narrowing gave only slight increase in yield. Weight of tops increases as row distance decreases.

(2) Spacings in the row from 6 to 12 in. produce no difference in yield of roots or sugar, and consequently the convenience of working with 12 in. makes that spacing distance the most desirable in practice.

(3) These experiments throw no light on the question as to whether optimum spacing is related to the level of fertility of the field; this very important practical consideration is being investigated.

The very laborious field work entailed in these experiments was carried out by graduate students, to whom the authors' thanks are due. All determinations of sugar percentage were made by the Advisory Chemist's Department, and it is a pleasure to acknowledge great indebtedness to Mr F. Hanley, M.A., for his willing co-operation.

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EXPERIMENTS ON THE SPACING OF SUGAR BEET

II. RESULTS BASED ON WEIGHTS OF INDIVIDUAL PLANTS

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(With Three Text-figures)

A DESCRIPTION of the experiments together with the results for, and conclusions drawn from, the plot yields has already been given (Garner & Sanders, 1939); the present paper is concerned with the results obtained, with roots and with tops, from the records of individual plants. A "perfect" beet was defined in the previous paper as a plant with no gaps in the ring of beet surrounding it, i.e. the two beets adjacent in the row, the two adjacent across the row and the four diagonal ones were all present.

In 1934, with only a 70 % average "plant", the number of "perfect" beet was low, and some plots carried none; in 1936 every plot carried some "perfect" beet, the number varying from 9 to 114. This provided a fair estimate for every plot (though clearly with varying precision) of the average size of roots which would have been obtained if there had been no gaps. The average weight of a "perfect" beet, multiplied by the number of beet sites which the spacing of the plot provided, produced an estimate of what the yield of the plot would have been had there been no gaps at all; this also involved the assumption that gaps beyond the first ring in no way affected the growth of a plant. Table I gives the estimated yields obtained in the above way, together with the number of beet upon which the calculation was based.

Despite the varying precision of the estimate of plot yield, the standard error of one plot yield calculated in this way was only 7.36 % of the general mean, a figure which would not be unreasonable in a normal experiment with sugar beet. As regards significance, the regression of yield of roots on distance between the rows reached the 5 % level, narrow rows giving the higher yield, but the deviations from linear regression were also significant at the same level. There was no significant difference between the 9 and 12 in. singling distances, but there was a highly significant interaction between the row distance and distance in the row. With the narrowest rows the wider spacings in the row gave the

higher yield, with 18 in. rows there was little to choose between the 9 and 12 in. spacings in the row, whilst with the 24 in. rows, 12 in. spacing in the row gave a yield very much lower than the 9 in. spacing. The practical conclusions from this table are very clear. Row distances

Table I. *Yield for different spacings estimated from weights of "perfect" beet, 1936*

Spacing in.	No. "perfect" beet in five plots	Estimated weight of roots in tons per acre	Estimated weight of tops in tons per acre
12 × 9	274	18.49	10.78
12 × 12	308	19.74	11.55
18 × 9	243	19.74	11.93
18 × 12	144	19.47	12.08
24 × 9	216	17.95	11.96
24 × 12	163	14.09	8.59
	Mean	18.25	11.15

should not exceed 18 in. and spacing in the row need be no less than 12 in.; if, on the other hand, distance between the rows is increased beyond 18 in. the loss of yield may be mitigated to some extent by reducing the spacing in the row to 9 in. But it is clearly unsafe to place much reliance on the figures in Table 1. Nuckols (1936) found that competitive beet (his term for what are here called "perfect" beet) gave unreliable estimates of the actual yields of experimental plots.

As regards weight of tops, the experimental error was high and no significant differences emerged.

In Fig. 1 the same results are expressed in graphical form, the abscissae being the area available to a perfect beet and the ordinates being the yields per unit area. The equations of the four curves fitted by the method of Isserlis, were:

$$\begin{aligned}
 1934: \quad \text{Roots} \quad y &= 2.054 + 0.00262x - 0.0000051x^2 \\
 &\quad \text{Tops} \quad y = 1.611 + 0.00040x - 0.0000022x^2 \\
 1936: \quad \text{Roots} \quad y &= 2.563 + 0.00678x - 0.0000207x^2 \\
 &\quad \text{Tops} \quad y = 0.827 + 0.01126x - 0.0000288x^2
 \end{aligned}$$

The curves show that in 1934 weight of roots was favoured by wide spacings and weight of tops by narrow, whilst in the wetter year of 1936 there was a fairly definite optimum spacing with regard to both; this was an allowance of 150-200 sq. in. per beet, which corresponds to a spacing of about 18 by 9 in.

A number of sugar analyses have been performed on the roots of individual "perfect" beet. In 1934 twenty-five such roots were taken from each of three plots and placed, after weighing, separately into paper

bags, in which they were transported to the laboratory for analysis; in 1936 more "perfect" beet were available, and forty were taken for individual sugar analysis from each of four plots.

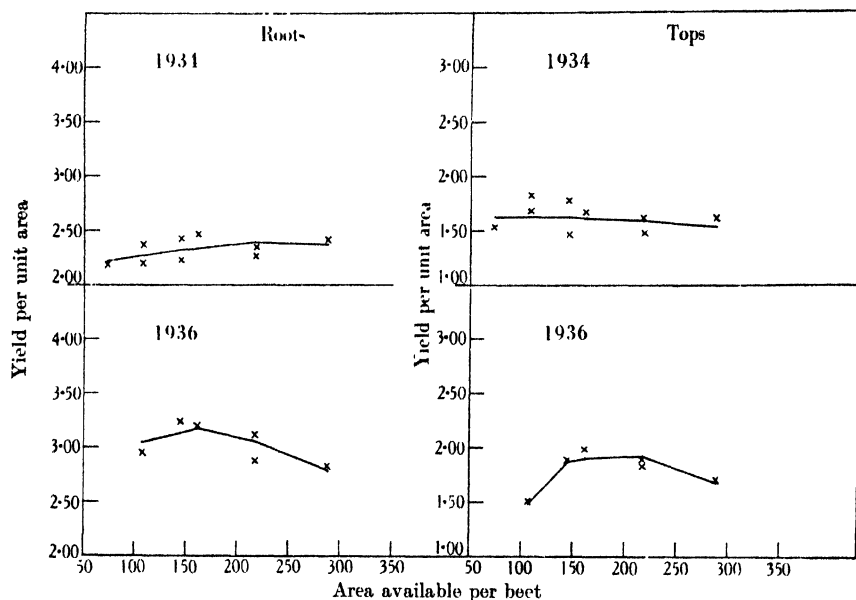


Fig. 1. Relation between yield and space available to each beet.
Based on perfect beet.

Table II gives the results obtained from the sugar analyses of individual "perfect" beet. The very small "perfect" beet produced by the closer spacings in 1934 showed positive correlations between sugar percentage and weight; the coefficient was significant in one case. It should be

Table II. "Perfect" beet. Relation between weight and
sugar percentage of root

Spacing in.	No. of beet tested	Mean wt. of root g.	Mean sugar %	Correlation coefficient r	Significance of r	Regression equation. Sugar % =
1934						
12 x 6	25	163	16.68	+0.451	$P < 0.02$	$15.84 + 0.005129W$
18 x 6	25	237	17.34	+0.124	Insig.	$17.11 + 0.000983W$
18 x 12	25	487	17.65	-0.171	Insig.	$18.13 - 0.000979W$
1936						
12 x 9	40	268	19.01	-0.054	Insig.	$19.31 - 0.001117W$
12 x 12	40	512	17.72	-0.206	Insig.	$18.47 - 0.001467W$
18 x 9	40	547	18.98	-0.336	$P < 0.05$	$20.06 - 0.001984W$
24 x 9	40	599	18.50	+0.197	Insig.	$17.87 + 0.001062W$

pointed out that the small beet whose low sugar content produced these positive correlations were very diminutive, some of them being so small as scarcely to justify lifting. If these small beet be excepted, the general indication is that weight and sugar percentage are negatively correlated, but the correlation coefficients were very small, and in fact only one of them was significant. From the regression equation shown in the table it is seen that sugar percentage only decreased by about unity for an increase of 1000 g. in weight of root. It seems justifiable to conclude that, over the ordinary range of root size, the relation between sugar percentage and weight is a very slight one, with little practical significance.

EFFECT OF GAPS ON WEIGHTS OF ROOTS AND TOPS

For each spacing (e.g. 12×6 in.) it was possible to arrange the individual plants into forty-five classes, according to the number of gaps in the ring of beet sites immediately surrounding them; this ring included two in the row, two across the row and four diagonally. The number of adjacent gaps in or across the rows could be 0, 1 or 2, whilst the number of diagonal gaps could be 0, 1, 2, 3 or 4, and it will be convenient to use the notation (a, b, c) to describe a beet with a adjacent gaps in the row, b gaps across the row and c gaps diagonally; in this notation (0, 0, 0) denotes a "perfect" beet. The beet were classified separately for each spacing treatment (the five replications being put together in this work), so that there were 405 possible classes for the 1934 data and 270 for the 1936 data; many of these classes had few or no representatives, and this was especially true of the wider spacings. It cannot be claimed that all the information obtainable from this classification has yet been extracted; the problem presents very considerable mathematical difficulties owing to very varying numbers falling in the classes, and to the possibility that size of neighbouring beet, rather than mere presence or absence, may be a determining factor.

As a first attempt to study the effect of varying sizes of gaps, situated at varying distances from the actual plant concerned, Tables III and IV were drawn up. All the mean weights shown in these tables are based on an appreciable number of plants; there were, with one exception, at least twenty-five individuals contributing to each mean shown in the tables, and the numbers in some cases were as high as 300. Both tables show that a gap in the row had a much larger effect than one across, or than a diagonal gap. Although in general the figures shown in Tables III and IV run smoothly some inconsistencies are observable, and Figs. 2

Table III. *Effect of gaps on average weight of individual roots (grams)*

Year	Spacing in.	"Perfect" beet (0, 0, 0)	1 gap in row (1, 0, 0)	1 gap across row (0, 1, 0)	Diagonal gaps	
					(0, 0, 1)	(0, 0, 2)
1934	12 × 6	158	221	167	174	197
	12 × 9	256	319	262	269	309
	12 × 12	350	421	441	343	395
	18 × 6	238	366	258	258	293
	18 × 9	399	504	432	409	372
	18 × 12	488	657	595	536	609
	24 × 6	321	515	298	328	342
	24 × 9	505	757	626	548	529
	24 × 12	702	911	697	700	783
1936	12 × 9	320	401	365	349	378
	12 × 12	466	504	506	470	531
	18 × 9	516	632	513	524	546
	18 × 12	671	831	717	630	743
	24 × 9	617	810	653	661	733
	24 × 12	819	1067	879	909	898

Table IV. *Effect of gaps on average weight of individual tops (grams)*

Year	Spacing in.	"Perfect" beet (0, 0, 0)	1 gap in row (1, 0, 0)	1 gap across row (0, 1, 0)	Diagonal gaps	
					(0, 0, 1)	(0, 0, 2)
1934	12 × 6	111	144	121	124	138
	12 × 9	181	205	185	193	202
	12 × 12	210	240	256	214	247
	18 × 6	197	270	218	202	218
	18 × 9	272	318	297	292	313
	18 × 12	320	362	379	376	371
	24 × 6	256	342	229	274	267
	24 × 9	351	472	408	371	385
	24 × 12	466	559	481	465	490
1936	12 × 9	180	219	221	211	237
	12 × 12	272	274	272	267	312
	18 × 9	321	338	324	307	338
	18 × 12	408	520	440	396	464
	24 × 9	393	448	434	444	439
	24 × 12	495	590	545	563	556

and 3 have been constructed in an effort to smooth out chance irregularities. By subtracting the mean weight for (0, 0, 0) beet from that of (1, 0, 0) beet, the effect of one gap in the row could be ascertained for the spacing concerned; in a similar manner the effect of one gap across the row could be determined. As regards diagonal gaps the estimates of a single gap, and also of two gaps, were available, and for weight of tops (0, 0, 2)–(0, 0, 0) was almost exactly double that of (0, 0, 1)–(0, 0, 0), whilst for weight of roots the former difference was over 50 % greater than the latter one; accordingly the effect of one diagonal gap was calculated as one-third of the sum of the two differences. From Fig. 2 it is seen at once that the effect of a gap across the row was considerably less than that of a gap in the row. Fig. 2*a* shows that the effect of a gap in

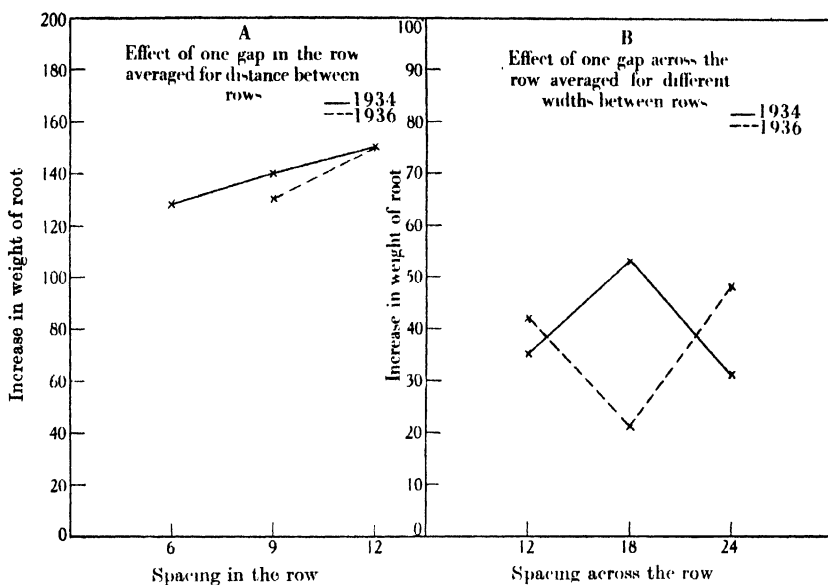


Fig. 2. Effect of single gaps in and across the row on weight of root.

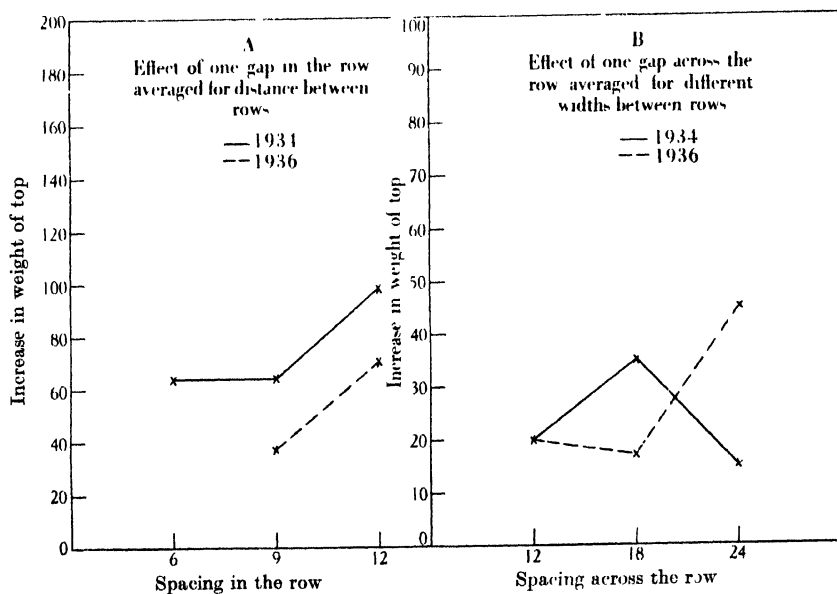


Fig. 3. Effect of single gaps in and across the row on weight of tops.

the row was large and that it increased with increasing spacing distance within the row. Fig. 2*b* shows that the increase in weight caused by a gap across the row was independent of row width; this is not surprising in view of the fact that even where a gap did occur across the row the plant still had another plant on each side of it, and usually closer to it, in the row.

Fig. 3 shows that, broadly speaking, weight of top was affected in the same way as weight of root, by gaps in and across the row, though with tops gaps across the row had nearly as great effect as gaps in the row.

The average value of the increase in weight of roots for one gap in the row was approximately 140 g., whilst the increase for one gap across the row was approximately 40 g. and for a diagonal gap 25 g.; for tops the corresponding figures were 67, 25 and 18 g. respectively. Clearly the effect of a gap on a near beet will be greater than that of a gap on a beet some distance away. In seeking a general rule a likely hypothesis might be that the effect was inversely proportional to the square of the distance between the surviving beet and the site from which a beet is missing. The average distance between rows was double the average distance within rows, and consequently on the above hypothesis gaps across the row might be expected to exert one-quarter of the influence of a gap in the row. With weight of roots this was approximately the result, though weight of tops did not conform very closely. On the same reasoning the effect of a diagonal gap might be expected to be approximately one-fifth of a gap in the row, and this is seen to be approximately the case. This is, perhaps, surprising, since it must be remembered that where there is a diagonal gap there will be two plants present closer to the beet concerned than the site of the gap and these two might be expected to exert greater competition, because they derive benefit from the gap. Despite irregularities the figures give some support for the above hypothesis.

If it is assumed, (a) that the effect of a gap on neighbouring roots is inversely proportional to the square of the distance of those roots from the empty root site, and (b) that the neighbouring plants entirely compensate by their extra growth for the plant missing in a single gap, it is possible to arrive at a figure to represent the space available for beet falling in every one of the above mentioned classes. The following example for the distance 24×12 in. will make the method clear. Let x be the effect on (i.e. space available to) a neighbouring beet in the row, y on one across the row, and z on a diagonal one; then for this spacing

$$144x = 576y = 720z.$$

If complete compensation occurs the summation of all space rendered available to neighbours must equal that available to one "perfect" beet; thus

$$2x + 2y + 4z = 288.$$

Solving these equations gives

$$x = 87.272, \quad y = 21.818, \quad z = 17.455,$$

and thus the space available for the following classes would be (in square inches):

$$(0, 0, 0) \rightarrow 288, \quad (1, 0, 0) \rightarrow 375, \quad (0, 1, 0) \rightarrow 310, \quad (0, 0, 1) \rightarrow 305, \\ (2, 1, 3) \rightarrow 537.$$

Separate tables were drawn up for the nine spacing treatments to show the space available for each class of beet.

It was possible to take from the sums of squares of deviations for weight, between the various classes of beet, a part ascribable to variations in the "space available" figure—i.e. the proportion of the sum of squares appropriate to the regression of weight on the space figure.

Table V. *Percentage of variation in weight ascribable to difference in calculated available space*

Spacing treatment	Roots		Tops	
	1934	1936	1934	1936
12 × 6	89	—	77	—
12 × 9	83	77	75	58
12 × 12	82	54	83	32
18 × 6	88	—	78	—
18 × 9	82	84	71	35
18 × 12	82	41	71	36
24 × 6	88	—	75	—
24 × 9	80	76	73	24
24 × 12	86	51	66	36

Table V shows that in 1934 the regression accounted for a high proportion of the variance between classes; this was particularly true as regards weight of roots. In 1936, however, the proportions were much lower. It seems possible that the difference between the two years may have been due to the very different climatic conditions. In 1934 the summer was hot and dry and growth was clearly restricted by lack of moisture, as was evidenced by the fact that the leaves on the closer spaced plots showed very distinct yellowing; in those conditions compensation for a gap was practically complete. In 1936 the rainfall was better distributed, and sufficient in amount for full growth on the closely spaced plots. It may be concluded that the inverse square rule, enunciated above, is justified under droughty conditions, but that the lessened effect

of a gap precludes its full operation in a wet year. From this it might be concluded that gaps would reduce yield to a greater extent on soils with a high water table than on others; general observation of sugar beet crops on fen soils, however, does not agree with this.

VARIATIONS WITHIN CLASSES

By no means all the variation between individual beet could be ascribed to differences in spacing or gappiness. There were very considerable variations between members of the same class, grown at the same spacing distances. The differences within classes must be ascribed to soil, or to genetic heterogeneity. Table VI shows, for each spacing distance and for each year, the coefficients of variation (i.e. $\sqrt{\text{mean squares within classes}}$ expressed as percentages of the general means) for both roots and tops.

Table VI. *Variation within classes*

Spacing treatment in.	Weight of root		Weight of top		Correlation coefficient (wt. root \times wt. top)	
	1934	1936	1934	1936	1934	1936
12 \times 6	50.81	—	46.05	—	+ 0.729	—
12 \times 9	45.82	40.76	45.36	48.15	+ 0.716	+ 0.663
12 \times 12	35.25	36.85	37.89	42.97	+ 0.668	+ 0.670
18 \times 6	47.91	—	44.61	—	+ 0.765	—
18 \times 9	35.33	37.30	38.73	44.23	+ 0.686	+ 0.718
18 \times 12	31.51	36.51	35.97	45.69	+ 0.669	+ 0.647
24 \times 6	50.70	—	41.81	—	+ 0.744	—
24 \times 9	38.69	38.57	40.20	49.52	+ 0.648	+ 0.673
24 \times 12	29.22	34.64	31.72	44.74	+ 0.632	+ 0.609

The Table shows that the variability was high and substantially similar with regard to both roots and tops; the coefficient of variation showed some reduction from the spacing treatments which produced many small beet to those which produced a few large beet. It has been shown earlier in this paper that plants can compensate to a large extent for gaps in their vicinity, and therefore it is improbable that this variability is caused to any appreciable degree by variation in soil. Thus it appears that genetic heterogeneity is responsible for a standard deviation in the neighbourhood of 40% of the mean. If this be accepted it becomes important in experiments with sugar beet (using commercial seed) to arrange that each plot carries an appreciable number of plants; thus in these experiments 64 would be necessary to reduce the plot error due to genetic variability to 5%, and 400 to reduce it to 2%, of the mean.

Further light on the variability between members of the same class is thrown by the correlation coefficients, calculated within classes,

between weight of root and weight of tops; these are also given in Table VI. Although all these correlation coefficients were highly significant, their general level of about 0.7 is surprisingly low; thus of the variation remaining between classes only one half could be eliminated by standardizing for weight of tops. This is in conformity with field observations which showed that even among beet similarly spaced, and similarly situated with regard to gaps, there were to be found great differences in size and shape.

SECOND RING GAPS

Most of the classes of beet were too sparsely occupied to admit of further subdivision, but in 1934 there were 11 classes with more than 80 beet each, and in 1936, 18 classes with more than 100 beet each; the beet in these classes were further classified according to the number of gaps in the ring of beet next but one to the plant in question, diagonal gaps being in this case neglected. Although one or two significant differences emerged, the general conclusion was that gaps in the second ring had very little, if any, effect, irrespective of presence or absence of beet in the first ring.

SUMMARY

1. Yields of plots estimated from the known weights of "perfect" beet (i.e. plants with no gaps in the ring immediately surrounding them) showed 18×9 in. to be the optimum spacing.

2. Sugar analyses performed on individual "perfect" beet showed that very diminutive roots were low in sugar, but that in general sugar percentage decreased with increasing weight of root; the decrease was, however, slight and only amounted to unity for an increase of 1000 g. in weight of root.

3. In a dry year the roots immediately surrounding a gap compensated to the extent of 80–89% for the missing plant: the allocation to the individual neighbours was approximately inversely proportional to the square of their distance from the site of the gap. In a wet year compensation was less complete, amounting to from 41 to 84% under various spacing treatments. In both years compensation was less complete in the case of tops than in the case of roots.

4. Within classes of beet similar in regard to spacing treatment and gappiness there still remained considerable variation due to soil and to genetic heterogeneity.

5. The genetic variability of commercial seed appears to be large, so that in sugar beet experiments it is very desirable that each plot should carry a considerable number of plants: in these experiments, assuming that all variations within ultimate classes were of genetic origin, 400 plants would have been necessary to reduce the plot error due to genetic variability to 2% of the mean.

Mr J. Grantham, M.A., has taken an active interest in the statistical reduction of the data, and his many useful suggestions are gratefully acknowledged.

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EXPERIMENTS ON THE SPACING OF SUGAR BEET

III. FURTHER STATISTICAL CONSIDERATIONS

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INTRODUCTION

THE effect of gaps on yield has already been considered (Part II) by examining the weights of individual beet. These weights were analysed according to the number and configuration of the surrounding gaps, but the effect of very small or very large beet in the ring or area under consideration was neglected. Extreme sizes of beet may produce effects comparable with that of a gap. This is borne out by the fact that in some spacings it was found that, if there were three or four diagonal gaps, the mean weight of the central beet was less than if all the surrounding beet had been present. This may be explained if the presence of the diagonal gaps causes the adjacent beet along and across the row to be larger than usual. Thus the central beet is surrounded by four beet whose size is above the average; this in turn tends to diminish its weight.

These considerations led to the feeling that a more satisfactory analysis would be obtained by studying the yield and gaps of an area covering about 10–30 beet sites. The effect on yield of gaps and other irregularities in the beet immediately surrounding the area under consideration is regarded as negligible, and is here neglected.

The relation between the yield and the number of gaps in a set of small areas will be considered. From this the yield for any percentage plant will be estimated. In particular the estimated yield for a field that does not contain any gaps (referred to below as a 100 % yield) will be compared with the corresponding estimates derived in Part II.

THE EFFECT OF GAPS ON YIELDS

In choosing a unit area three considerations had to be borne in mind:

(1) The area should be large enough for the effects of gaps and other irregularities in the surrounding areas to be negligible.

(2) There should be enough unit areas to permit accurate statistical analysis; hence the areas must not be too large.

(3) If possible, each area should contain an integral number of beet in each spacing.

The unit area adopted was 72×36 inches; for each area the following data were recorded:

- (1) The spacing and the number of beet.
- (2) The number of beet, expressed as a percentage (x) of the total number of beet possible in that area; referred to as "percentage plant".
- (3) The number of gaps.
- (4) The number of gaps in the surrounding ring of beet.
- (5) The yield (y), or total weight of roots, in grams.

For each spacing the yields of the 80 areas were grouped into arrays according to the number of plants in the area, and an analysis of variance made as follows:

Variation due to	Degrees of freedom	Sums of squares
Regression of y on x	1	$b^2 \sum n_i (x_i - \bar{x})^2$
Deviations of array means from regression	$p - 2$	$\sum n_i (Y_i - \bar{y})^2$
Deviations within arrays	$N - p$	$\sum \sum (y - \bar{y}_i)^2$
Total	$N - 1$	$\sum \sum (y - \bar{y})^2$

where p = number of arrays,

n_i = number of areas in the i th array,

$N = \sum n_i = 80$,

x_i = the value of x for the i th array,

\bar{x} = the mean x ,

\bar{y}_i = the mean yield in the i th array,

\bar{y} = the mean yield,

$b = \sum n_i (x_i - \bar{x}) (y_i - \bar{y}) / \sum n_i (x_i - \bar{x})^2$,

Y_i = value of the mean yield in the i th array, calculated from the regression equation

$$Y_i = \bar{y} + b (x_i - \bar{x}).$$

The mean squares with degrees of freedom $p - 2$ and $N - p$ were not significantly different in any spacing, so that no significant departure of the regression line from linearity can be detected. Hence these two sets of degrees of freedom were combined, and the resulting mean square used as an estimate of the variance about the regression line. Comparison of the mean squares due to regressions with those due to deviations from the regression lines showed that in every spacing, with one exception (the 18×6 inch spacing in 1934), the regression coefficients were positive and significant.

Table I. *Regression of yield on percentage plant. Values of b*

Distance between the rows in.	Distance between plants in a row					
	1934			1936		
	6 in.	9 in.	12 in.	9 in.	12 in.	
12	17.4	19.5	34.9	44.3	70.5	
18	8.6	34.7	33.6	58.9	55.9	
24	17.3	33.0	49.2	60.7	50.4	

Table II gives the estimated yields for a given percentage plant for unit areas. They depend on the general level of fertility, so that comparisons can only be made within each experiment. The standard errors for each value of x may be computed from

$$\text{s.e. of } Y = S \sqrt{\left(\frac{1}{80} + \frac{(x - \bar{x})^2}{\sum n_i (x_i - \bar{x})^2} \right)},$$

where

$$S^2 = \frac{1}{78} \sum \sum (y - \bar{y})^2,$$

in which y and Y are the observed yield and the point on the regression line corresponding to the percentage plants x . The values corresponding to $x=100$ are given in Table III.

Table II. *Estimated yields of unit areas for different percentage plants*

Spacing in.	Percentage plant								
	100	95	90	85	80	75	70	60	50
1934 experiment									
12 × 6	<i>6180</i>	6100	6010	5920	5840	5750	5660	5480	5310
12 × 9	<i>6430</i>	6330	6230	6140	6040	5940	5840	5650	5450
12 × 12	6810	6630	6460	6280	6110	5930	5760	5410	5060
18 × 6	<i>6030</i>	<i>5980</i>	5940	5900	5860	5810	5770	5680	5600
18 × 9	6840	6660	6490	6310	6140	5970	5800	5450	5100
18 × 12	6830	6660	6500	6330	6160	5990	5820	5490	5150
24 × 6	<i>6070</i>	<i>5980</i>	<i>5900</i>	5820	5720	5640	5550	5380	5200
24 × 9	6470	6300	6140	5980	5810	5650	5480	5150	4820
24 × 12	6940	6690	6450	6200	5960	5710	5460	4970	4480
1936 experiment									
12 × 9	8260	8040	7820	7590	7370	7150	6930	6480	<i>6040</i>
12 × 12	8780	8430	8080	7720	7370	7020	6670	5960	<i>5260</i>
18 × 9	8540	8240	7950	7650	7360	7060	6770	6180	5590
18 × 12	8260	7980	7700	7420	7140	6860	6580	6030	5470
24 × 9	7900	7590	7290	6990	6680	6380	6080	5470	4860
24 × 12	7890	7640	7380	7130	6900	6630	6380	5870	5370

Values in italics are extrapolated.

CONSIDERATION OF ESTIMATED YIELDS IN FIELDS WITH
NO MISSING BEET

The yield of a plot without any gaps can be estimated by two methods, one of which is to consider the so-called perfect beet, whose mean may be taken as an estimate of the yield of a perfect plant. However, since there will, in general, be some gaps in the second ring, the beet in the first ring will tend to become large, and thus cause the yield of the central beet to become subnormal. Hence the estimate derived in this way tends to be too low.

The other method is to use the regression lines already discussed. This tends to give an over-estimate, since the yields of very dense areas are increased by less dense areas surrounding them; this causes the regression coefficients to be too large. The yields by both methods are compared in Table III.

Table III. *Estimated yields of a field with no missing beet*

Spacing in.	1934 experiment			1936 experiment		
	Perfect beet	Regression		Perfect beet	Regression	
		Yield	S.E.		Yield	S.E.
12 × 6	5690	6180	220	—	—	—
12 × 9	6140	6430	220	7770	8260	260
12 × 12	6290	6810	140	8290	8780	200
18 × 6	5690	6030	240	—	—	—
18 × 9	6390	6840	180	8300	8540	190
18 × 12	5850	6830	190	8180	8260	230
24 × 6	5770	6070	220	—	—	—
24 × 9	6060	6470	170	7540	7900	150
24 × 12	6310	6940	170	5920	7890	100

These two sets of estimated yields are consistent, except those for the 24 × 12 inch spacing in 1936, in which the perfect beet method has certainly given a bad estimate; in fact this estimate is less than the observed mean yield. It may be remarked that the perfect beet method takes into account only a sample which may, from the very nature of the method by which it is chosen, be considerably biased; the regression method, on the other hand, utilises all the available data. The general conclusion is that the best spacing is about 18 × 9 or 18 × 12 inch.

To test the effect of neglecting the ring around the unit areas, the correlation coefficients between the yield of an area and the number of gaps in the surrounding ring were evaluated for each of the fifteen spacing classes. The means of these correlations were 0.143 in 1934, and 0.031 in 1936. These are quite small; that for 1934 is unduly large

because a number of areas in the 18×6 inch spacing (which was the only one to show a non-significant regression) gave anomalous results. This shows that the effect of leaving out of consideration the gaps in the surrounding ring was negligible.

RANDOMNESS OF GAPS

It is of some interest to know whether the gaps are distributed in a random manner. Three methods were used to analyse the gaps for certain types of departure from a random arrangement.

(1) Assume that the probability of a gap is p , where p is constant for all positions in the field. In all areas which could contain n beet, the numbers of gaps will be distributed with frequencies proportional to the terms of the binomial $(p+q)^n$, where $q=1-p$.

The field was divided into rectangular areas which did not overlap, containing nine beet sites, and also into areas containing four beet sites. For each area the number of gaps within it was recorded and for each spacing the number (n_r) of areas with r gaps was counted. Now Cochran (1936) has shown that, if the gaps are random, then

$$\frac{n \Sigma n_r (r - \bar{r})}{\bar{r} (n - \bar{r})}$$

is distributed as χ^2 with $m = (\Sigma n_r) - 1$ degrees of freedom, where \bar{r} is the mean number of gaps per area.

The values of m and $\xi = \sqrt{(2\chi^2)} - \sqrt{(2m-1)}$ are given in Table IV. Since m is ≥ 79 , ξ can be taken to be normally distributed about zero with unit standard deviation. The values of χ^2 can be combined according to distance between or within the rows to give Table V. Many of the

Table IV. *Values of $\xi = \sqrt{(2\chi^2)} - \sqrt{(2m-1)}$ from the distributions of gaps*

Spacing in.	Areas with four beet sites				Areas with nine beet sites			
	1934		1936		1934		1936	
	D.F.	ξ	D.F.	ξ	D.F.	ξ	D.F.	ξ
12 x 6	1039	2.89 ss	—	—	319	6.35 ss	—	—
12 x 9	719	3.05 ss	719	1.06	219	4.88 ss	299	0.15
12 x 12	559	1.96 s	559	0.04	159	2.57 s	224	1.35
18 x 6	779	1.24	—	—	239	0.90	—	—
18 x 9	539	3.76 ss	539	2.61 ss	164	2.98 ss	239	2.63 ss
18 x 12	419	2.28 s	419	1.97 s	119	0.80	179	2.60 ss
24 x 6	649	3.01 ss	—	—	254	1.42	—	—
24 x 9	449	1.00	449	2.41 s	109	1.81	179	1.75
24 x 12	349	0.26	349	1.65	79	1.11	134	0.95

s means significant at 5%. ss means significant at 1%.

values are highly significant and there seems no doubt that the gaps are not random.

Table V

Areas with four beet sites						Areas with nine beet sites					
1934			1936			1934			1936		
D.F.	ξ		D.F.	ξ		D.F.	ξ		D.F.	ξ	
Distance between rows:											
12 in.	2317	4.55	ss	1277	0.88		697	7.85	ss	522	0.96
18 in.	1737	4.12	ss	957	3.24	ss	522	2.78	ss	417	3.69
24 in.	1447	2.72	ss	797	4.13	ss	442	2.41	s	312	1.93
Distance within rows:											
6 in.	2467	4.12	ss	—	—		812	4.08	ss	—	—
9 in.	1707	4.79	ss	1707	4.29	ss	492	5.86	ss	717	2.46
12 in.	1327	2.71	ss	1327	2.03	s	357	2.69	ss	537	2.92

(2) An analysis of variance was made on the percentage of gaps in each plot, in the form appropriate to a split plot experiment, and is given in Table VI.

Table VI. *Analysis of variance of the percentage of gaps in plots*

Variation	1934			1936		
	D.F.	S.S.	M.S.	D.F.	S.S.	M.S.
Blocks	4	44.97	11.24	4	17.74	4.43
Inter-row distances	2	2.32	1.16	2	3.88	1.94
Error (<i>a</i>)	8	53.56	6.69	8	6.38	0.80
Main plots	14	100.86		14	28.00	
Intra-row distances	2	15.95	7.97	1	1.37	1.37
Interaction	4	1.99	0.50	2	3.77	1.88
Error (<i>b</i>)	24	34.44	1.44	12	10.84	0.90
Total	44	153.24		29	43.98	

The mean square corresponding to variations between blocks is significantly greater than error (b) at the 1 % level both in 1934 and 1936. It is also greater than error (a) at 5 % in 1936. The only variation between spacings which is significant is between inter-row distances in 1934.

This means that the percentage of gaps varies over the field but it is not much affected by the spacing of the beet.

(3) If the gaps are at random, the correlation between the number of gaps in each of the unit areas used above, and the number of gaps in the ring around should be zero. These correlations are shown in Table VII and many differ significantly from zero. This supports the previous conclusions that the distribution of gaps varies considerably over the field. It may be noticed that the variability appears, according to all three methods, to have been less in 1936 than in 1934.

Table VII. *Correlation between the gaps in a unit area and the gaps in the surrounding ring*

Distance between rows in.	Distance within the rows					
	6 in.		9 in.		12 in.	
	1934		1934	1936	1934	1936
12	0.42	ss	0.58	ss	0.22	s
18	0.22	s	0.33	ss	0.27	s
24	0.22	s	0.19		0.32	ss

A fourth method was attempted, by considering the distribution of runs of gaps along and across the row. The mathematical form of this distribution in the case of short rows could not be obtained in a suitable form. It was hoped by this method to determine whether there were any differences which could be separated from the general properties of the field.

SUMMARY

1. The distribution of the total weight of beet in small areas (2 yards by 1 yard) was examined and estimates made of the effects of missing beet on the final yield, and of the yield to be obtained with various percentage plants.

2. The distribution of gaps over the field is found to be non-random. The percentage of gaps varies from block to block, but does not differ greatly between the spacings. Three methods were employed and gave consistent results.

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POPULATION STUDIES WITH WHEAT

I. SAMPLING

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(With Fifteen Text-figures)

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I. INTRODUCTION TO THE SERIES

IN the last twenty years it has come to be regarded as essential in every agricultural experiment that errors of experimentation should be accurately estimated. More recently, however, it has been realized that to measure differences in crop yield produced by experimental treatments, whatever the statistical precision, is of limited investigational value. It is necessary to know how treatment affects yield, and this can only be revealed by measuring the influence of treatment on plant development at various stages of growth. Under field conditions such developmental studies must be simple, e.g. with cereals density of plant population, amount of tillering, or number of ears. On large plots it is impracticable to make such observations on every plant, and sampling must therefore be employed. In a replicated plot experiment any treatment mean which

is estimated by sampling will be liable to an error of sampling in addition to the normal experimental error, and this extra error naturally increases the total error of the experiment and the amount by which the observed mean may deviate from the true mean. Very little practical work has been done on this problem, and, apart from the work of Clapham (1929, 1931), and the mainly theoretical considerations of Yates & Zaccopani (1935), little is known either of the increase of experimental error caused by sampling, or the best method of reducing it. That such errors are often very large is proved by certain cereal experiments at Cambridge, where results obtained when harvesting by sample differed from those obtained when the remainder of each plot was harvested, and correlations between sample yields and "plot" yields were low and often insignificant.

In 1933 a bequest under the will of the late Miss M. S. Greg became available to finance a large-scale investigation of the sampling problem, and the experiments were so arranged that the problem of "propinquity" could be investigated from the same data. This is the problem of the extent to which the population density at one point affects growth and yield at immediately adjacent points. Besides being of very great theoretical interest, this has a practical bearing on such problems as the relationship between irregularities of seed distribution by coulter of the drill and yield. Engledow & Ramiah (1930), in attempting to measure this effect in spacing trials and census studies, have met with conflicting results, and Fairfield-Smith (1937), working in Australia, has encountered similar difficulties.

These two problems, sampling and propinquity, were investigated by dividing a continuous area of wheat, sown as a field crop in accordance with normal farm practice, into a large number of adjacent small areas or "units", and recording the plant number, stem number, yield, etc., for each unit. Two such experiments have been made. The first was drilled in November 1934 under the supervision of G. B. Laurence, Ph.D., now of the Department of Agriculture, Pretoria, who developed the field technique, and was also responsible for some of the earlier calculations on the sampling problem; the second was drilled in December 1935 on a different site on the University Farm, Cambridge. Each experiment consisted of a continuous piece of wheat divided into five "strips" of 1440 units of 6 in. of drill row, giving in all 7200 units of $6 \times 7\frac{1}{2}$ in. in each experiment. Each unit was observed for seven characters in the case of the first experiment, and for six in the second. In all $7200 \times 13 = 93,600$ individual observations were made, and in the course of the computations it was necessary to evaluate over $1\frac{1}{2}$ million products—a task only made

possible by the use of Hollerith equipment (Comrie, 1937). These figures may help to give some idea of the scale on which this work was done.

It is proposed to publish the results of this investigation as a series, of which this paper, which deals with the sampling problem, is the first.

II. EXPERIMENTAL PROCEDURE, AND DESCRIPTION OF CROP

The field technique and lay-out of the experiments to be described were designed so that not only values of plant number, etc., for 7200 units of 6 in. of drill row of wheat might be obtained but also the position of each unit, and the values for adjacent units. Since correlations between various plant attributes were required, it was necessary that each unit should be permanently marked, so that the position of the area might be exactly the same at each observation.

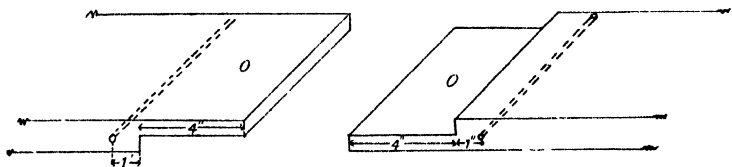


Fig. 1. Method of joining planks in forming "grid".

The wheat for the first experiment was drilled on 14 November 1934 after potatoes, and a specially stiff-strawed variety, now released by the National Institute of Agricultural Botany under the name of Holdfast, was used to minimize the risk of lodging. The soil was a light loam; the field level and near a farm road. By early January the experimental area was ready for a plant count, but before this could be made the site had to be chosen and marked out. The area was divided into five "strips" 72 ft. long and ten rows wide, each containing 1440 units whose positions were permanently marked out by means of a "grid" of cross-wires running at right angles to the drill rows; a discard of one drill row was left between each strip. The grid was made in the same way for all strips; first two lengths of planking 1 in. \times 4 in. \times 24 yd., with holes bored at 6 in. intervals across the 4 in. width, were laid alongside the two outside discard drill-rows. The whole length was made by bolting together three or four individual planks, the join being made by an overlapping method which ensured that the holes on either side of the join were exactly 6 in. apart (see Fig. 1). These were fixed in position on the plot side by driving in pegs in the positions shown in Fig. 2. The grid

was then completed by lacing a thin steel wire (piano wire was used) through the holes and to and fro between the planks as shown. It was found that since it cut into the wood the wire did not slip once it had been pulled tight.

The actual counting was done from solid wooden "bridges", 8 ft. long by 4 ft. 6 in. wide, standing 9 in. off the ground on four wooden legs which were so placed that they could be rested on the planks on both sides. A team consisted of two counters and a booker; the counters lay side by side on this bridge, and each counted the five rows immediately

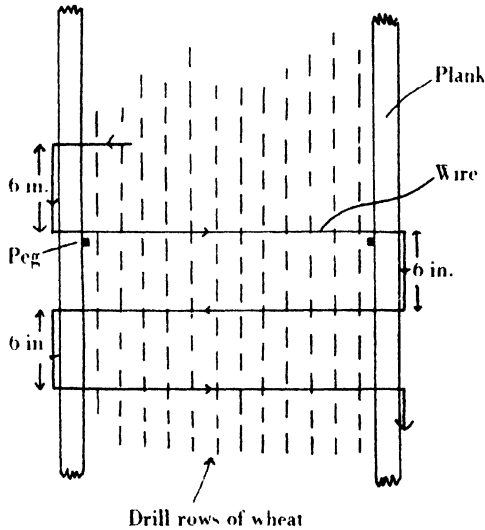


Fig. 2. The formation of the "grid".

in front of him, the figures being taken down in the correct order by the booker, who was able to keep up with both counters, and at the same time check the position of each unit. The figures were entered in field books, and copied on to large sheets of squared paper in the laboratory.

Tiller counts were made in March and April 1935, the same technique being used. The accuracy of the first count was considerably affected by the inclement weather and the fact that it took place at an early stage in the tillering process; many small tillers were present, and it was difficult to assess the minimum size of tiller and to ensure that all counters had the same standard. The figures given by this count were discarded.

At harvest the following information was obtained for each unit:

- (1) Number of plants.
- (2) Number of ears.
- (3) Weight of grain.
- (4) Weight of straw.

In order that the number of plants might be counted at threshing the plants of each unit was pulled up by the roots. This could easily be done by hand, and no preliminary loosening of the soil was necessary. The ears from each unit were placed inside a flour bag, 4 × 9 in. in size, which had previously been perforated by small holes which permitted aeration but through which grain could not escape; this ensured that the grain should not go musty.

Threshing was commenced on 19 August. First the number of plants in each unit was determined. To do this the earth was removed from the roots, so that they could be separated out without splitting. Experience showed that a satisfactory count could be made in most cases if the earth was removed by striking the roots against a solid object; in difficult cases, however, it was necessary to soak the roots in water. The roots were then cut off at a point comparable with that at which a binder cuts, and the total produce weighed to the nearest $\frac{1}{10}$ g. The weight of the flour bag, strings, and a label which was attached to each unit was allowed for by counterbalancing. The bag was then removed, and the number of ears and of green ears counted. These were then cut off and placed in small linen bags, 6 × 4 in., and threshed by beating against some solid object. The bag was then emptied into a sieve, the chaff removed, and the grain weighed. Each of the five readings were written on the back of the label, which accompanied the unit throughout its travels, even being in the bag when threshing occurred. Finally, the readings were copied into the appropriate positions on the sheets of squared paper. It was found that a gang of three could thresh 400 units in a 7 hr. day.

This experiment was repeated in 1935-6 on a different field of similar soil type. It was drilled on 2 December 1935; the germination count was made on 3 March, and only one tiller count was taken, in mid-April. Although the site was carefully chosen, a band of fertility running across the strips appeared in May. The difference between this band and the remainder of the experiment became so pronounced that it had to be harvested separately a week after the major part of the experiment. It gave a yield of 47·8 bushels/acre—very nearly double the yield of

25.1 bushels/acre given by the rest of the experiment. The average yield for the experiment was 33.8 bushels/acre, which was very similar to the yield from the 1934-5 experiment, 35.5 bushels/acre.

The means of the various plant attributes in both years are given in Table I.

Table I. *Means of the various plant attributes per foot of drill row in 1934-5 and 1935-6*

	1934-5	1935-6
No. of plants at germination	17.42	21.76
No. of stems in April	56.44	40.26
No. of ears at harvest	18.34	21.14
Wt. of grain in g.	14.55	13.89
Wt. of straw in g.	23.80	25.44
Yield in bushels/acre	35.50	33.80

In addition to differences between the averages set out in Table I the type of variation among the yields in the two years shows a marked

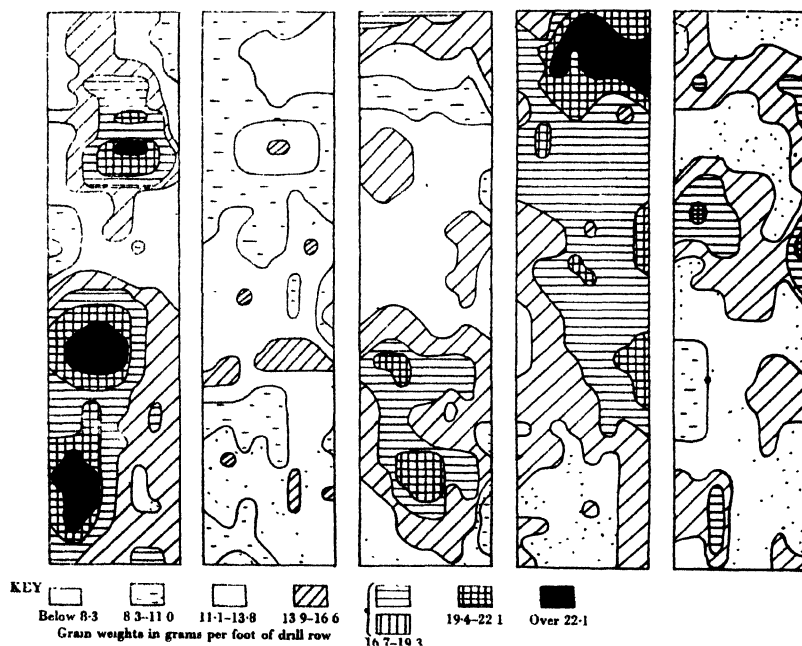


Fig. 3. Fertility contour map 1934-5, based on moving averages for yield of grain from areas of 2 ft. \times 1 drill row.

difference. This is shown in Figs. 3 and 4, where a "contour map" of the grain yield in the two years is given. The map was formed in the usual way, 2 ft. lengths being taken as the unit. It is not strictly to scale, and

shows that marked trends of fertility occurred in both years, but that the direction of the trend varied. In 1934-5 the patches of high fertility

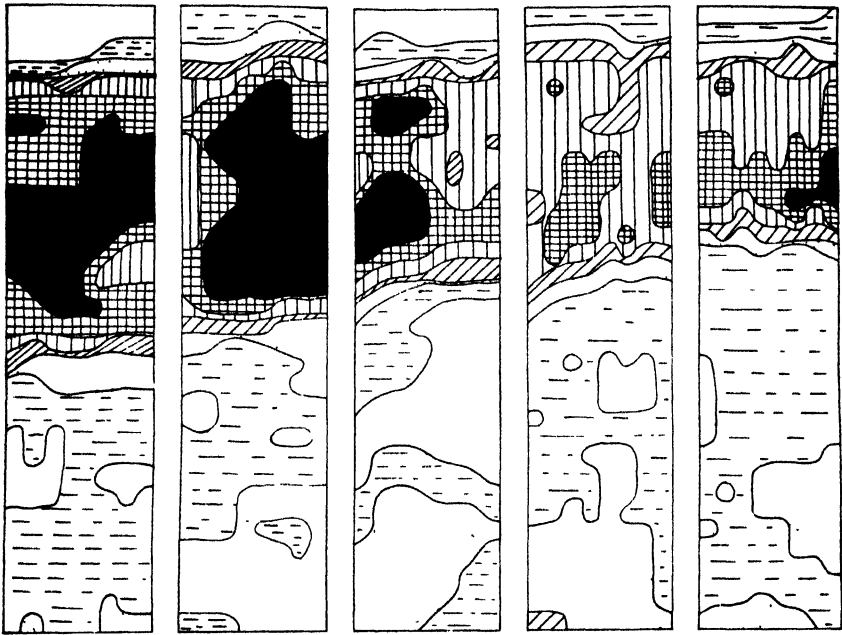


Fig. 4. Fertility contour map 1935-6, based on moving averages for yield of grain from areas of 2 ft. x 1 drill row. Key as for Fig. 3.

occurred, running along the strip, but in 1935-6, when the difference was very noticeable, the area of high fertility ran across the strip.

III. THE SAMPLING PROBLEM

(1) *Introduction*

There are various reasons why sampling methods have to be used in experimental work; in field experiments they are employed mainly to save labour. That such a reduction of labour is necessary when developmental counts are to be made has been shown in the introduction, and this is the reason for the majority of sampling. Sometimes, however, factors of personnel, time available, size and number of plots, capacity of the threshing machine, and transport make a small bulk desirable even when the yield only is required. An important particular case of this is where experiments are situated on "outside farms", at

some distance from a suitable threshing machine, when the cost of transport becomes an important consideration. For these reasons sampling must frequently be employed, and since sampling introduces an extra error, the factors influencing this error must be known in order that it may be kept as low as possible.

The accuracy of any sample of wheat is affected by the percentage of the plot taken, the size and shape of the sampling unit, the degree of subdivision of the plot, and the nature of the plant attribute observed. Earlier workers have made no attempt to separate these effects, although work has been done on the problem of cereal sampling by Clapham (1929), who emphasized the necessity of *random* sampling and advocated subdivision of the plot, and later (1931) evolved a technique for obtaining a sampling error of 5-6 % for grain weight and straw weight from plots of about 1/50 acre, by Kalamkar (1932), and by Yates & Zacopanay (1935). The experiments now described were designed to remedy this deficiency. On the assumption that it entails less labour to handle a small increase of total produce when the number of sampling units is thereby decreased, these experiments show that the optimum size of sampling unit for any plant attribute is 6 ft. of drill row, taken as 3 ft. of two adjacent rows. The size of the sampling unit is more important than the shape (provided that extremes of length and breadth are avoided), and little is lost by taking a sampling unit of 18 in. of five adjacent rows. This agrees with the work of Kalamkar (1932), who investigated the effect of shape with a sampling unit of a fixed size (2 m. of row) and found that four adjacent $\frac{1}{2}$ m. rows were optimum. These results may also be contrasted with those of Christidis (1931), who found that long narrow plots had the lowest standard errors. This evidence, however, is not strictly comparable in this connexion since he was working with larger plots. Both Clapham and Yates & Zacopanay note that the proportion of the plot taken as a sample ought to grow as the plot size decreases, and this is found to be true and capable of mathematical expression. With regard to the effect of the nature of the plant attribute, it is found that grain weight requires the largest sample, and, since it is normally necessary to sample all attributes to the same extent, the requirements of grain weight become the determining factor.

It has been found that there is considerable uncertainty with regard to the meaning of the terms in the "vocabulary of sampling", and opportunity is taken to restate these. In order to sample the yield, say, of a plot, a number of small areas chosen at random are harvested.

These areas are called the *sampling units*, and are of the same size and shape. The sum of these sampling units is called the *sample* of the plot. The *sampling percentage* is the total area included in the sample expressed as a percentage of the area of the whole plot. The *sampling error* (Wishart & Sanders, 1935) is given by the expression

$$s = \sqrt{\left(\frac{v}{p} (1-f)\right)},$$

where v is the variance between sampling units, p the number of sampling units in the plot, and f the fraction of the plot taken as the sample. It is usually expressed as a percentage of the mean of the sampling units, and gives a measure of the variation of the plot mean due to sampling. In practice a sampling error of 5% means that, with a population whose mean determined by sampling is m , there is a 19:1 chance that the true plot mean will lie between $m + \frac{5m \cdot 2}{100}$ and $m - \frac{5m \cdot 2}{100}$, e.g. within the range $\frac{1}{5} m$.

(2) *The sampling unit*

(a) *Optimum width.* The object of the investigation is to find the optimum method of sampling for the characters observed. To do this it is necessary to decide (a) the optimum size and shape of sampling unit for each character, and (b) the number of such sampling units to take to obtain a given accuracy. The optimum size of sampling unit is most practicably obtained by first deciding the optimum width in terms of numbers of rows, and then determining the optimum length of the given width.

If the results for each observation were given in each stage the number of figures and tables would become excessive. For this reason the statistical methods are described in detail only for grain weight in 1934-5, and the final results are given for the remaining observations. The first step was to form populations of sampling units of various sizes and shapes. This was done by combining adjacent units as follows: the grain weight from the 7200 6 in. lengths were first added down the row (see Fig. 5) in twos and threes to give the grain weight of 3600 12 in. "singles" and 2400 18 in. "singles" respectively, and across the row in pairs, fives and tens to give the grain weight of 3600 6 in. "pairs", 1440 6 in. "fives", and 720 6 in. "tens". The figures obtained were then added horizontally in pairs and threes to form populations of 1800 12 in. pairs, 1200 18 in. pairs, 720 12 in. fives, 480 18 in. fives, 360 12 in. tens, and 240 18 in. tens. Addition of the grain weights for adjacent areas was continued until thirty-two populations for areas of various sizes had

been formed (see Table II). In Fig. 5 a diagrammatic representation of the field is given, each line representing a unit. The sampling units shown are 6 in. pairs, 12 in. fives, 18 in. singles, and 6 in. tens.

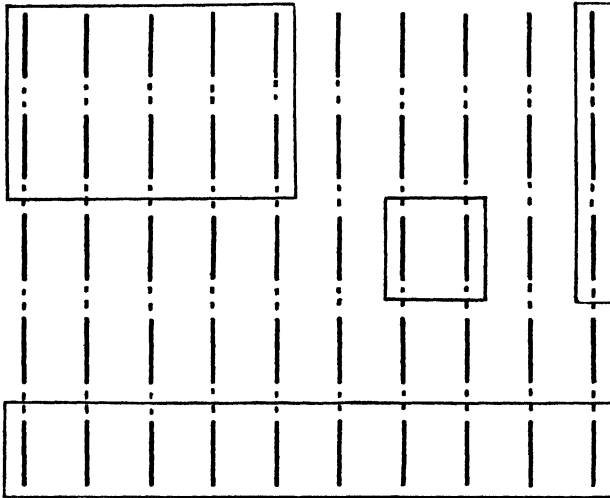


Fig. 5. Diagrammatic representation of part of field to illustrate formation of various size sampling units. Area shown: 10 rows \times 2 ft. 6 in.

The frequency distribution of the units was not normal, β_1 being $+0.97$ and $+1.62$ and β_2 1.62 and 5.17 in 1934-5 and 1935-6 respectively. The frequency distributions of 12, 18, 24 and 36 in. singles were also obtained, and it was found that the larger the sampling unit the more normal the distribution became within the range examined.

Table II. *To show the size and nature of the various populations formed*

Length in in.	Singles		Pairs		Fives		Tens	
	No. of rows	Size of population	No. of rows	Size of population	No. of rows	Size of population	No. of rows	Size of population
6	1	7200	2	3600	5	1440	10	720
12	1	3600	2	1800	5	720	10	360
18	1	2400	2	1200	5	480	10	240
24	1	1800	2	900	5	360	10	180
36	1	1200	2	600	5	240	10	120
48	1	900	2	450	5	180	10	90
72	1	600	2	300	5	120	10	60
144	1	300	2	150	5	60	10	30

The standard error for each size of sampling unit, expressed on a 6 in. length basis, was then determined and plotted, on logarithmic paper, against the number of units in the sampling unit, and the points given

by the eight "singles", eight "pairs", eight "fives", and eight "tens", joined up separately, giving four lines (Fig. 6). The standard error is the best criterion of the accuracy of the mean obtained from the sampling units. If the area of the sampling unit is held constant, the lower the standard error the greater this accuracy. These graphs show that for any given size of sampling unit containing more than 5 ft. of drill row it is best to take sampling units in the form of strips right across the drill width. This is also shown in Fig. 7, which is another method of

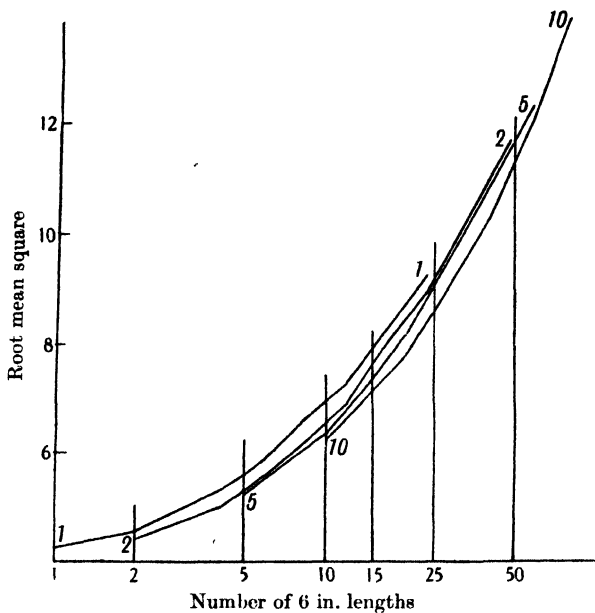


Fig. 6. To show the relationship between size of sampling unit and the root mean square. Graphs for singles (1), pairs (2), fives (5) and tens (10) shown separately.

presenting the data shown in Fig. 6. Each graph in Fig. 7 represents the relation between root mean square (R.M.S.) and width of sampling unit with area of sampling unit held constant. The size of this area is marked on each graph in terms of number of units. Each line passes through four points, all of which are given by sampling units of the same area. The shape of the area, however, varies; the first point shows the R.M.S. for sampling units of 1 row \times x ft., the second for 2 rows \times $x/2$ ft., the third for 5 rows \times $x/5$ ft., and the fourth for 10 rows \times $x/10$ ft. Each line in Fig. 7 shows the relative position of the lines for singles, pairs, fives and tens in Fig. 6 for a given size of sampling unit—the vertical lines in

Fig. 6 showing where the "cross-sections" have been taken. The lowest point on each of these lines gives the optimum width for a given size of sampling unit, and it is clear that, provided the sampling unit consists of more than 10 units, "tens" give the lowest error.

The above computations were for grain weight in 1934-5. Similar computations were also made each year for

- (1) Number of plants at germination.
- (2) Number of stems in April.
- (3) Number of plants at harvest.¹
- (4) Number of ears at harvest.
- (5) Grain weight in g. at harvest.
- (6) Straw weight in g. at harvest.¹
- (7) Weight of total produce in g. at harvest.¹
- (8) Grain/total produce ratio at harvest.¹

This involved finding the sums of squares for each population, and necessitated the squaring of $32,400 \times 12 = 388,800$ numbers. In addition to this sums of products for each combination of observations for each year in each size of sampling unit were required for a correlation study which is not included in this paper. This necessitated the formation of 1,166,400 further products, making 1,555,200 in all. This task was only made possible by the use of Hollerith calculating machines, on which much of the work was done. A full account of these machines and of the technique used has already been published (Comrie, 1937).

The results are summarized in Figs. 8*a*, *b* by graphs similar to those in Fig. 7: those shown in Fig. 7 are included for the sake of completeness.

The results from the two experiments, and from the various plant attributes in each experiment, differ widely. The graphs for grain weight have a regular slope—a drop from left to right in 1934-5 and from right to left in 1935-6; those for plant number at germination, stem

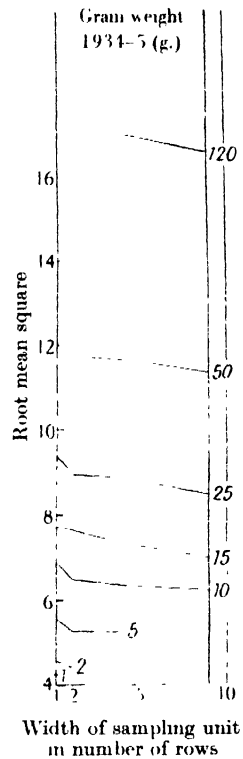


Fig. 7. Regression of root mean square on width of sampling units for various sizes of sampling units. The figures on the right show the size of sampling unit (in terms of the number of units included) represented by each line. Figures for grain weight in 1934-5.

¹ Results for (3), (6) and (7), being of secondary interest, are not given or discussed; (8) is treated separately.

number and ear number have minima whose value varies from graph to graph.

The influence of the size and shape of sampling unit is clearly not the same for every plant attribute. Consequently it is impossible to arrive at a conclusion which will be valid for all attributes, since for

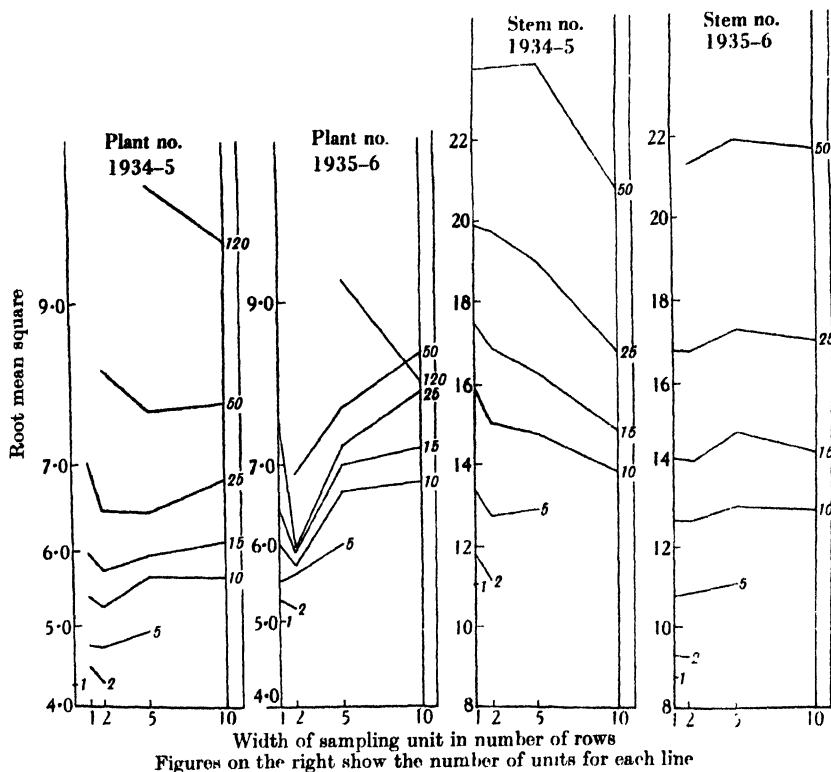


Fig. 8a. Regression of root mean square and width of sampling units for various sizes of sampling units. The figures on the right show the size of sampling unit (in terms of the number of units included) represented by each line. Graphs for plant number and stem number in both years.

practical purposes all must be sampled in the same manner; thus any statement of the optimum width will necessarily be a compromise, arrived at by a consideration of that width which is optimum in the majority of cases, and which will not cause undue loss of information in the remainder. In 1934-5 pairs are best for the germination count, tens for the stem count, pairs or fives for ear number, and for grain weight; where the differences are smaller, tens are best. In 1935-6 the

situation is different; pairs are best for every observation except grain weight, when singles seem to be slightly better (Fig. 8*b*). The difference between the results from the two years is caused by the difference in the direction of the trend of fertility, already illustrated in Figs. 3 and 4. In 1934-5 the trend ran across the area and favoured tens, and 1935-6

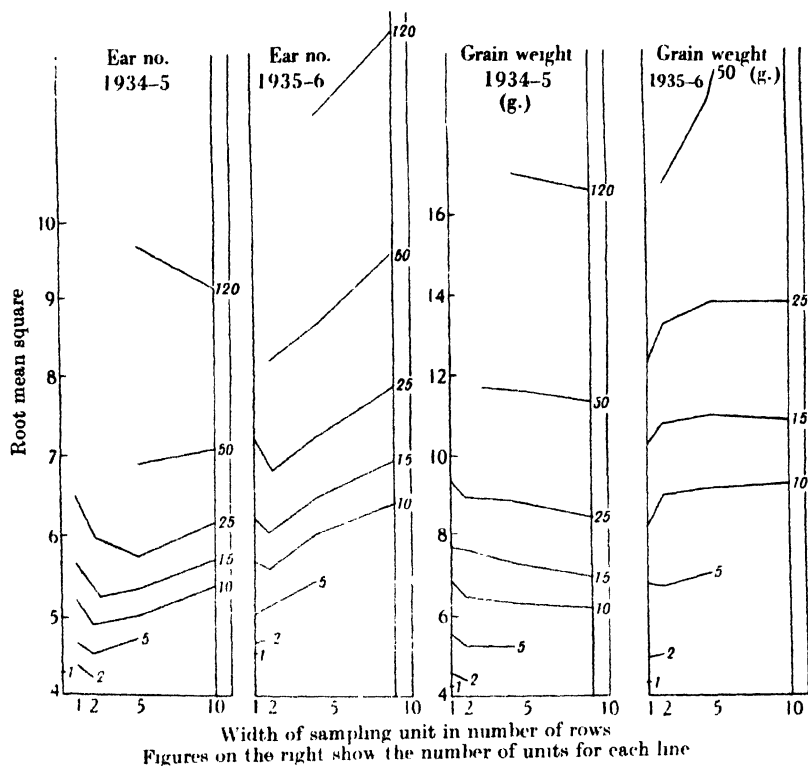


Fig. 8*b*. Regression of root mean square and width of sampling units for various sizes of sampling units. The figures on the right show the size of sampling unit (in terms of the number of units included) represented by each line. Graphs for ear number and grain weight in both years.

down the strips, favouring singles. A consideration of the results for both years indicates that "pairs" is the optimum width of sample, but that little is lost by taking fives.

(*b*) *Optimum length.* Having found that the optimum width of sampling for lengths ranging from 6 in. to 12 ft. is two rows, the problem of finding the optimum size and shape of sampling unit becomes that of finding the optimum length of pairs of rows, which, in its turn, is the

problem of finding the optimum size *using only pairs of rows*. To do this it is necessary to work out the relationship between the standard error of the population of sampling units, and a quantity hereinafter denoted by F , defined as the percentage of the plot that must be taken as a sample in order to obtain a sampling error of 5% of the mean, and then to find how F varies with different sizes of sampling unit.

Let us consider a sampling unit of n units. If there are p of these in the sample, and the variate under consideration is x , then the standard error of the sample must be

$$\sqrt{v} = \sqrt{\frac{\Sigma(x - mn)^2}{p - 1}},$$

where m is the mean of the variate for a unit.

Now we have defined the sampling error as $\sqrt{\left(\frac{v}{p}(1-f)\right)}$ (see p. 84), and, if this is to be 5% of the mean (mn) of the variate in question, we must have

$$\sqrt{\left(\frac{v}{p}(1-f)\right)} = \frac{5mn}{100},$$

whence

$$p = v(1-f) \times \left(\frac{100}{5mn}\right)^2.$$

Now, since $F = 100f$, we have

$$F = \frac{100np}{7200} = \frac{100^3}{m^2 \cdot 25 \cdot 7200} \frac{v}{n} \left(1 - \frac{F}{100}\right).$$

The first term, which may be written

$$k = \frac{100^3}{m^2 h s^2},$$

is a constant for any variate observed in unit plots, of which the mean is m , with h units in the aggregate, and working to a sampling error of $s\%$.

Solving for F we obtain

$$F = \frac{kv}{n} \left(\frac{100}{100 + \frac{kv}{n}} \right).$$

The values of F giving a sampling error of 5% of the mean for different lengths of pairs of rows for the various observations in both years are given in Table III, which also gives values of N , the number of sampling units necessary to give $F\%$ of the plot. It will be seen that if F were the only criterion of the efficiency of a sampling unit, then the

smaller the sampling unit the more efficient it would be. This is shown in Fig. 9 in which graphs of the sampling percentage (F) \times the size

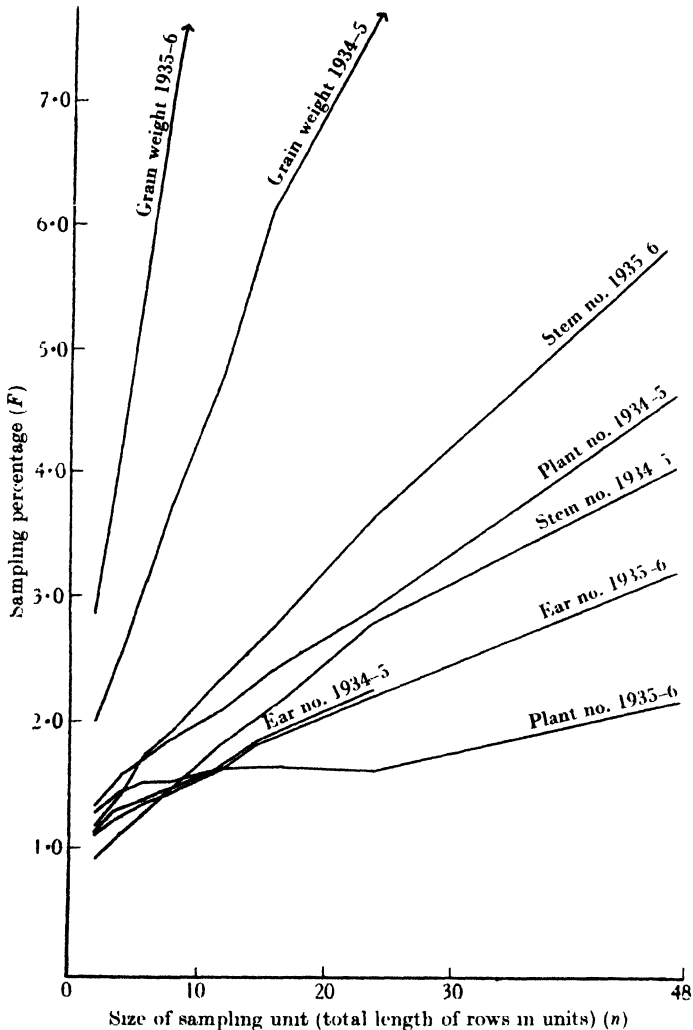


Fig. 9. Graphs of the sampling percentage \times the size of sampling unit for various observations.

of sampling unit are represented. This relationship appears to be linear in every case except one, which shows that, for a given increase in the size of the sampling unit there is a proportionate increase in the percentage of the plot that must be taken. The slope of each line (b in

Table III) gives a direct measure of the increased percentage that must be taken for each unit increase in the size of sampling unit when sampling for the various characters.

Table III. *Values of F (the percentage of the plot which must be sampled to give a 5% sampling error), and of N (the number of sampling units required to obtain $F\%$ of the plot), for the various values of n , the number of "units" in the sampling unit. Data for pairs of rows only, and for various observations. b is the regression coefficient of F on n*

		No. of units in sampling unit n									
		2	4	6	8	12	16	24	48		
Length of pairs	in in. ...	6	12	18	24	36	48	72	144		
Observation											b
Germination count:											
1934-5	F	1.34	1.56	1.72	1.86	2.09	2.40	2.89	4.57	0.0687	
	N	48	28	21	17	13	11	9	7		
1935-6	F	1.26	1.44	1.51	1.52	1.63	1.64	1.62	2.15	0.0161	
	N	45	26	18	14	10	7	5	3		
Stem count:											
1934-5	F	0.93	1.12	1.28	1.51	1.82	2.18	2.78	4.00	0.0670	
	N	33	20	15	13	11	10	8	6		
1935-6	F	1.17	1.42	1.75	1.91	2.34	2.73	3.62	5.75	0.0988	
	N	42	26	21	17	14	12	11	9		
Ear no.:											
1934-5	F	1.15	1.28	1.38	1.47	1.65	1.85	2.24	—	0.0486	
	N	41	23	17	13	10	8	7	—		
1935-6	F	1.10	1.23	1.35	1.44	1.63	1.83	2.20	3.18	0.0448	
	N	40	22	16	13	10	8	7	5		
Grain weight:											
1934-5	F	2.00	2.52	3.11	3.72	4.75	6.11	7.60	12.40	0.226	
	N	72	45	37	33	29	27	23	19		
1935-6	F	2.86	4.20	5.73	7.11	9.92	12.35	16.41	23.96	0.492	
	N	103	76	69	64	60	56	49	36		

In field experiments practical experience has shown that N , the number of sampling units to be taken from each plot, has to be considered in addition to the percentage, F , to be sampled, and that it is worth increasing the amount of material handled if by doing so the number of sampling units can be reduced. Reasons for this may be tabulated:

(1) The time spent locating sampling units is very considerable, especially if they have been marked out by pegs or wires which are often difficult to find at harvest. If they are not so marked, the position of each has to be found by measurement at each observation, which means that errors of measurement may occur, and exactly the same area will not be observed on each occasion.

(2) At harvest it is necessary to put the ears of wheat from each sampling unit into a perforated paper bag to minimize loss of grain, and

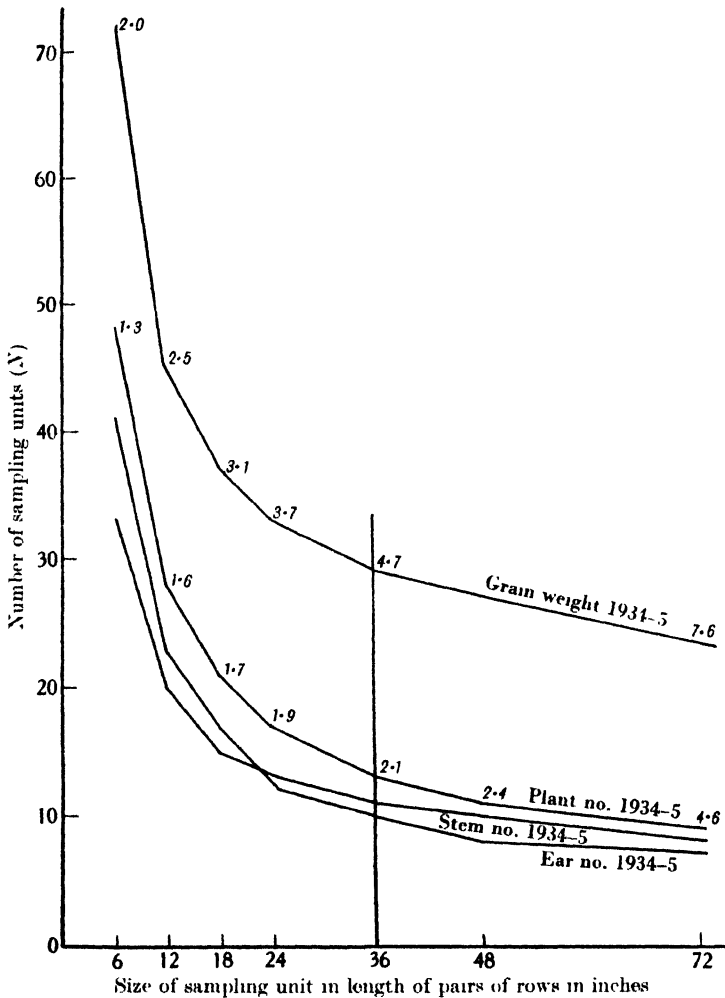


Fig. 10. Number of sampling units required to give a 5% sampling error \propto size of sampling unit for various observations in 1934-5. Figures on the lines show F , the percentage of the plot that must be taken, at various points.

to label each unit separately, should the sampling error be required. It is found that the largest sampling unit that can be handled with accuracy and which will dry satisfactorily is about 8 ft. of drill row. A reduction in the number of sampling units not only lessens the work

of "bagging" but reduces the number of labels to be written, and thus the chance of a mistake in labelling.

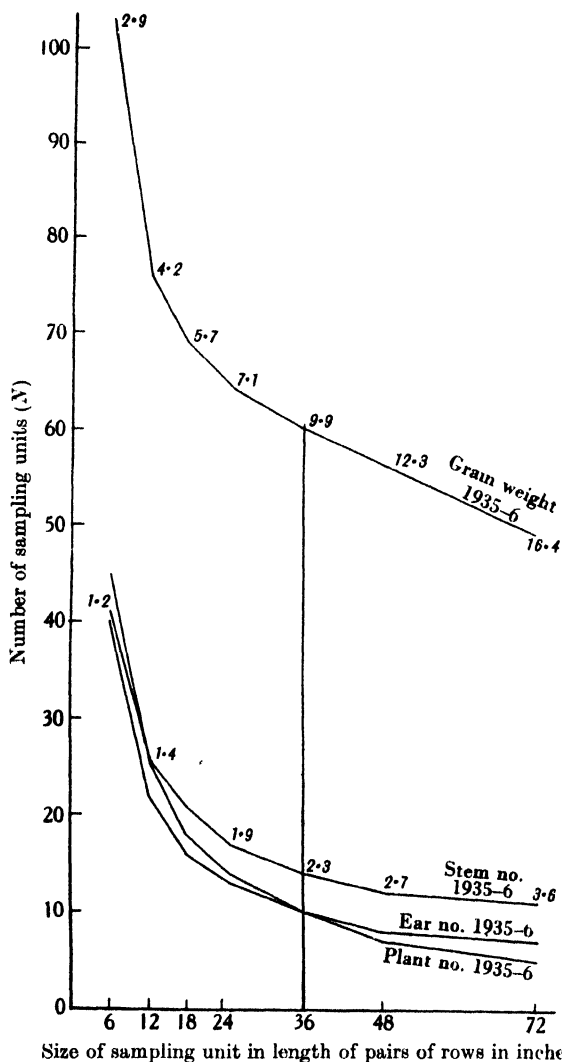


Fig. 11. Number of sampling units required to give 5% sampling error \times size of sampling unit for various observations in 1935-6. Figures on lines show F , the percentages of the plot that must be taken, at various points.

(3) When threshing, the number of times the machine has to be cleaned out, and the number of weighings and entries which have to be made, influence the rate of progress considerably.

(4) Final sample totals are obtained by adding the contributions of the individual sampling units. The fewer there are of these the quicker will this be done, and the less the chance of error.

(5) The error of edge effect, which may be considerable in cases where positions are fixed by measurements only, is reduced by the decrease in N .

If the number of sampling units necessary (N) is plotted against the size of sampling unit (n) (which will give a graph similar in shape to graphs of $N \times F$, since the relationship between F and n is linear) a curve is obtained which falls rapidly at first, but levels out as the values of n increase (Figs. 10, 11). An argument similar to that used by Mercer & Hall (1912) may be applied. With small sampling units the reduction in the number of sampling units to be taken for an increase in the size of sampling unit (and thus an increase in the percentage to be handled) is considerable. The larger the sampling unit the less this drop, until, after 3 ft. pairs, very little decrease results from an increased size of sampling unit. Thus it is worth taking the larger 3 ft. pairs, even though an extra percentage of the plot has to be sampled, because of the smaller number of sampling units that may be taken; when, however, the size of sampling unit is increased above this, the reduction in the number of sampling units is not large enough to compensate for the additional percentage of the plot that must be observed.

There is considerable divergence between the sampling percentages of the various observations, but in all cases (with the possible exception of grain weight in 1935-6), though the percentage of the plot that must be taken varies, the optimum size of sampling unit remains the same. These experiments show that the optimum size of sampling unit for the various characters of wheat investigated is 3 ft. of two adjacent rows, 6 ft. of drill row. The size of sampling unit is of greater importance than the shape, and it can be shown that little is lost by taking a sampling unit of 18 in. fives (7½ ft. of drill row) which is the optimum length if fives be considered instead of pairs (for grain weight in 1934-5 $F=5.30$ and $N=25$ with 18 in. fives, compared to $F=4.75$ and $N=29$ for 3 ft. pairs). This conclusion supports that of Kalamkar (1932) who found that ½ m. lengths of four adjacent rows (about 6 ft. of row) gave the best sampling unit.

(3) *The sample*

(a) *Influence of nature of observation.* The percentage of plot to be sampled varies from observation to observation (see Table III). In both

years the highest percentage has been required by grain weight, and the figure obtained from the 1935-6 data must be regarded as a limiting value, since all observations must be sampled to the same extent. This shows that 10% of a plot of 1/20 acre should be taken (see Table III). It is felt, however, that in view of the pronounced fertility strip running through the 1935-6 experiment, this may be considered an unusually high figure which will allow for the most improbable irregularities, and that a sampling percentage of 5%, as given by the more normal 1934-5 experiment, will generally give sufficient accuracy. Arguments in support of this assumption are given later in this paper. If grain weight is not to be sampled the limiting factor is the germination count in 1934-5, requiring a sampling percentage of 2.1, and the stem count in 1935-6, requiring a percentage of 2.7.

(b) *Influence of size of experimental plot.* An analysis of variance technique was used to obtain the standard error for various sizes of sampling units within experimental plots smaller than the whole experiment. Table IV illustrates the method used to obtain the standard error of 3 ft. pairs within strips, double microplots (D.M.P.) (12 ft. \times 10 rows), and microplots (M.P.) (6 ft. \times 10 rows) for grain weight in 1934-5.

Table IV. *Example of calculation of R.M.S. for sampling units within plots smaller than the whole experiment. Figures for grain weight in 1934-5*

	Plot area (acres)	D.F.	S.S.	M.S.	R.M.S.	F
Between 3 ft. pairs	—	599	28,503.71	47.585	6.8982	4.75
Between strips	1/97	4	7,989.61	—	—	—
Between D.M.P.	1/581	29	14,644.72	—	—	—
Between M.P.	1/1162	59	16,112.09	—	—	—
Between 3 ft. pairs within strips	—	595	20,514.10	34.477	5.8717	15.32
Between 3 ft. pairs within D.M.P.	—	570	13,858.99	24.314	4.9309	43.35
Between 3 ft. pairs within M.P.	—	540	12,391.62	22.947	4.7903	59.09

Fig. 12 shows the regression of standard error within double microplots on size of sampling unit for grain weight in 1934-5. The position of the lines for lengths, pairs, fives and tens, with regard to each other naturally remains unaltered, since a fixed quantity has been subtracted from the standard error of all populations of sampling units of the same size. The graphs of $N \times$ size of sampling unit (Fig. 13) also retain their initial shape, showing that the optimum size of sampling unit is not affected by plot size, but N decreases. The percentage of the plot to be sampled, F , increases rapidly, being 4.75 for 1/20 acre plots, 15.32 for 1/97 plots, and 43.3 for 1/581 acre plots. If plot size (x) be measured in terms of microplots (1/1162.8 acre), the relationship between the sampling

percentage and the size of experimental plot is accurately represented by $1/F = 0.0199 + 0.3209x$. It is interesting to note that when the doubtful procedure of calculating values of F for values of x outside the range observed is carried out, it is found that 0.26% should be taken from 1 acre, and 0.026% from 10 acres. The value for 10 acres agrees with that obtained by Cochran (1938), who found that he obtained sampling errors of from 8 to 14% by taking 1/15,000 of a 10-acre field, with sampling units totalling $4\frac{1}{2}$ m. of row.

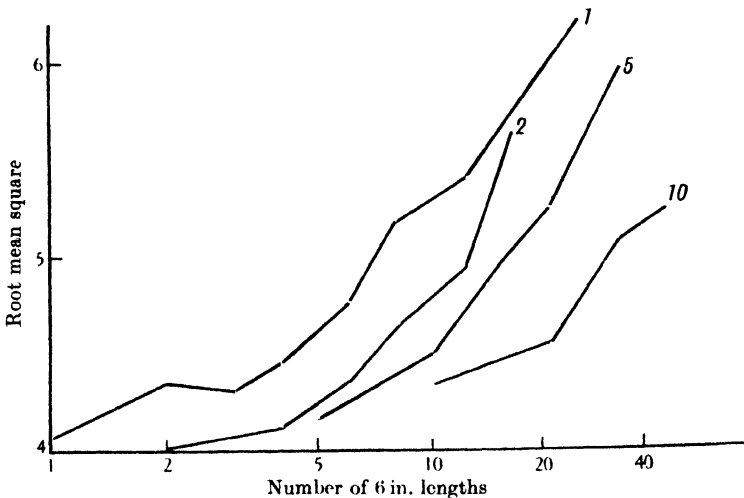


Fig. 12. To show the relationship between size of sampling unit and root mean square. Graphs for singles (1), pairs (2), fives (5) and tens (10) within double microplots.

The large variation is due to the method of measuring the sampling error in terms of the mean. With a plot yield of 1000 g. an error of 50 g. would satisfy the demands of 5% sampling, but with a plot yield of 100 g. such an error would give a 50% sampling error. If a 5% sampling error is required we must so arrange the sampling as to obtain a 5 g. error within samples. The rapid increase of F observed occurs because the standard error within samples does not fall proportionally as the plot yield: it is found that reducing the size of plot by 1/5 and 1/30 only reduces the error by 1/1.2 and 1/1.5 respectively. When the variation in both directions is removed by considering double microplots (a method analogous to the latin square method of experimentation), the two experiments give similar results. With such small plots it becomes necessary to take a sample of about half the plot.

Tables of the values of N for various sizes of sampling unit in various sizes of plots for germination count and stem number in the two years are given in Table V; in these cases divergences are not so great.

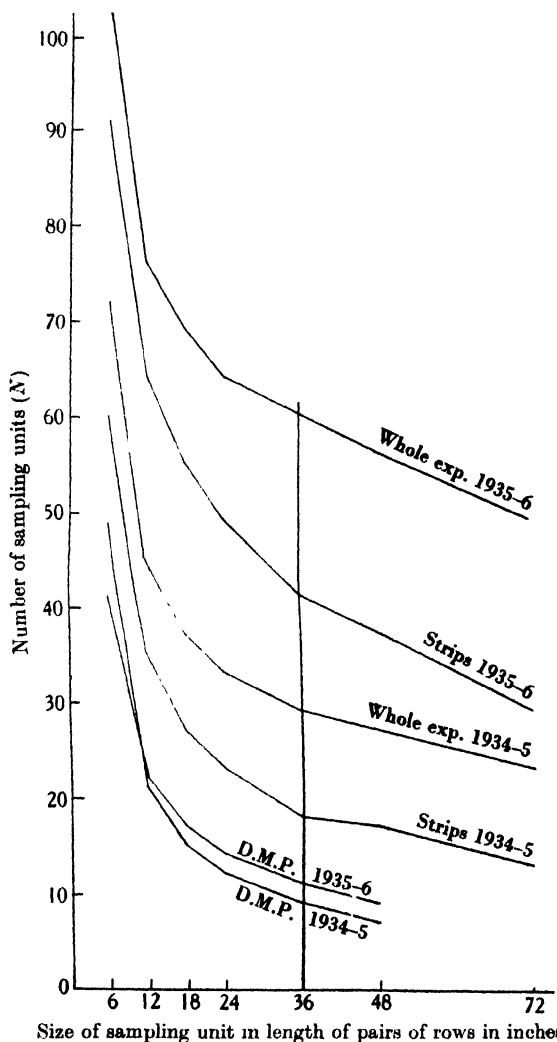


Fig. 13. Number of sampling units required to give a 5% sampling error \times size of sampling unit for grain weight in various sizes of plot.

(c) *Influence of division of plot for sampling.* The practice of dividing the plots for sampling and taking an equal number of sampling units from each subdivision reduces the sampling percentage considerably.

Table V. *Values of N for germination count and stem no. in 1934-5 and 1935-6 for various values of "n" in plots the size of the whole experiment, strips and D.M.P.*

		No. of units in sampling unit <i>n</i>							
		2	4	6	8	12	18	24	48
Germination: 1934-5	Whole exp.	48	28	21	17	13	11	9	7
	Strips	44	22	18	14	10	8	6	5
	D.M.P.	33	18	12	10	7	5	4	—
1935-6	Whole exp.	45	26	18	14	10	7	5	3
	Strips	43	24	17	13	9	7	4	3
	D.M.P.	40	22	15	11	7	6	4	—
Stem count: 1934-5	Whole exp.	33	20	15	13	11	10	8	6
	Strips	31	18	13	11	9	8	6	4
	D.M.P.	25	14	10	8	7	5	4	—
1935-6	Whole exp.	42	26	21	17	14	12	11	9
	Strips	39	21	16	13	10	8	7	5
	D.M.P.	28	15	11	8	6	4	3	—

This reduction occurs because any variation between the divisions of the plot is annulled by the fact that an equal area is taken from each, and it is only the small variation within these divisions that adds to the uncertainty of the sample. Thus variation between divisions may be eliminated from the error between sampling units much as the block variation may be eliminated from error in a randomized block experiment. Table VI illustrates the analysis of variance technique used in determining an improved estimate of *v* from which improved values of *F* and *N* are calculated for grain weight in 1934-5 from the whole experiment, using 3 ft. pairs, (a) when no subdivision is made, (b) when an equal number of sampling units are to be taken from each strip, and the effect of subdividing plots the size of (a) the whole experiment, and (b) strips, is shown in Figs. 14 and 15.

Table VI. *Example of calculation of F and N for sampling units with and without subdivision. Figures for grain weight in 1934-5*

	D.F.	S.S. (on unit basis)	M.S.
Between strips	4	7,989.61	—
Between 3 ft. pairs within strips	595	20,514.10	34.477
Between 3 ft. pairs	599	28,503.71	47.585

$$(a) F = 47.585 \times \frac{100}{100 + 47.585 \times 0.1049} = 4.75; N = 29.$$

$$(b) F = 34.477 \times \frac{100}{100 + 34.477 \times 0.1049} = 3.49; N = 21$$

$$k = \frac{100^2}{7.277^2 \times 7200 \times 25} = 0.1049.$$

Table VII. *F* and *N* for various observations using a sampling unit of 3 ft. pairs

Size of plot and degree of subdivision	Plant no.		Stem no.		Ear no.		Grain wt.	
	1934-5	1935-6	1934-5	1935-6	1934-5	1935-6	1934-5*	1935-6
(a) Values of <i>F</i>								
Whole exp.:								
None	1	2.09	1.54	1.82	2.34	1.43	1.63	4.75 [✓]
Strips	5	1.78	1.52	1.60	1.76	1.29	1.44	3.49 [✓]
Half-strips	10	1.65	1.51	1.56	1.36	1.27	1.35	2.92
Strips:								
None	1	8.30	7.16	7.51	8.21	6.14	6.82	15.32
Half-strips	2	7.73	7.12	7.34	6.45	6.06	6.39	13.07
D.M.P.	6	7.55	6.87	6.92	6.26	5.89	5.43	11.31
Half-strips:								
None	1	14.31	13.29	13.68	12.13	11.43	12.01	23.12
M.P.	6	13.86	12.32	12.37	11.27	11.19	9.26	19.40
D.M.P.:								
None	1	32.9	37.1	30.8	28.6	27.3	25.6	43.3
(b) Values of <i>N</i>								
Whole exp.:								
None	1	13	9	11	14	9	10	29
Strips	5	11	9	10	11	8	9	21
Half-strips	10	10	9	9	8	8	8	18
Strips:								
None	1	10	8	9	10	7	8	18
Half-strips	2	9	8	9	8	7	8	16
D.M.P.	6	9	8	8	8	7	7	14
Half-strips:								
None	1	9	8	8	7	7	7	14
M.P.	6	8	7	7	7	7	6	12
D.M.P.:								
None	1	7	7	6	6	5	5	9

* Recommended values.

Table VII gives the sampling necessary to give a 5% sampling error, using sampling units of 3 ft. of two adjacent drill rows, for

(a) Plots equal in size to the whole experiment (1/20 acre) taken without division, and with division into strips and half-strips.

(b) Plots equal in size to strips (1/97 acre) taken without division, and with division into 1/2 and 1/6.

(c) Plots equal in size to half-strips (1/194 acre) taken without division, and with division into 1/6.

(d) Plots equal in size to D.M.P. (1/581 acre), taken without division.

The figures in column 8 (grain weight, 1934-5) show values of *F* which will usually give satisfactory sampling either for individual characters or for a series of observations on the wheat crop.

Figures giving a sampling error other than 5% may be obtained by multiplying the figures given in Table VII by $(5/x)^2$, where *x* represents the desired sampling error, expressed as a percentage of the mean. Thus

the sampling percentage that would give a 10% sampling error is obtained by multiplying by $(5/10)^2 = 25/100$, i.e. dividing by 4.

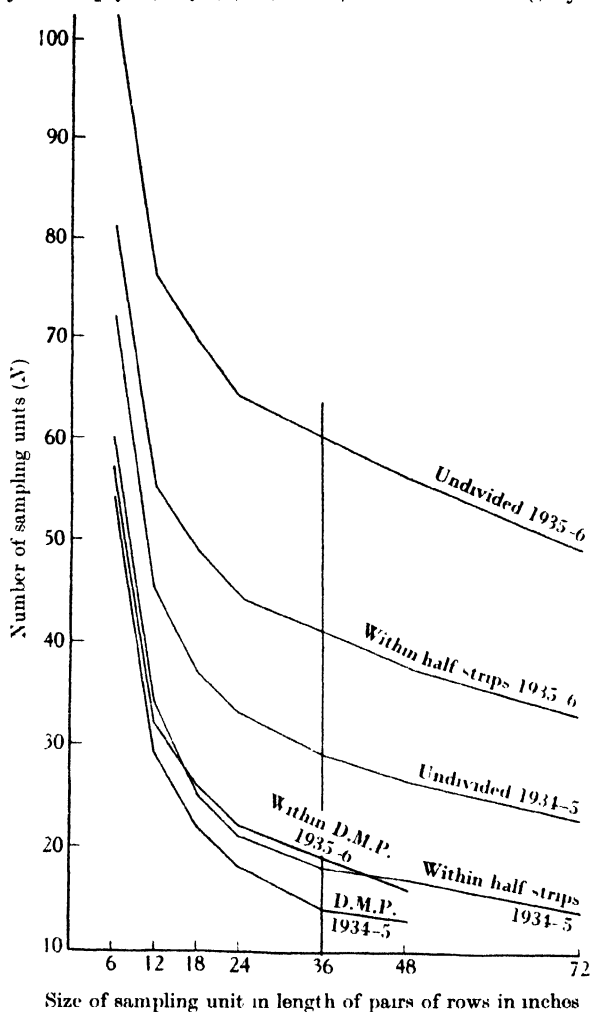


Fig. 14. Graphs of $N > n$ for various subdivisions of the whole experiment. To show the amount of sampling necessary to obtain a 5% sampling error from plots the size of the whole experiment (1/19 acre).

The subdivision of plots for sampling decreases the error considerably, especially in cases where there is a large fertility effect. Figs. 14 and 15 and Table VII both show that the greater the degree of subdivision the lower is the percentage necessary to give a 5% sampling error for any given degree of sampling. This effect is so great that, even in the case

of observations affected by the "fertility strip", the degree of sampling is not excessive provided the plots are sufficiently subdivided. In

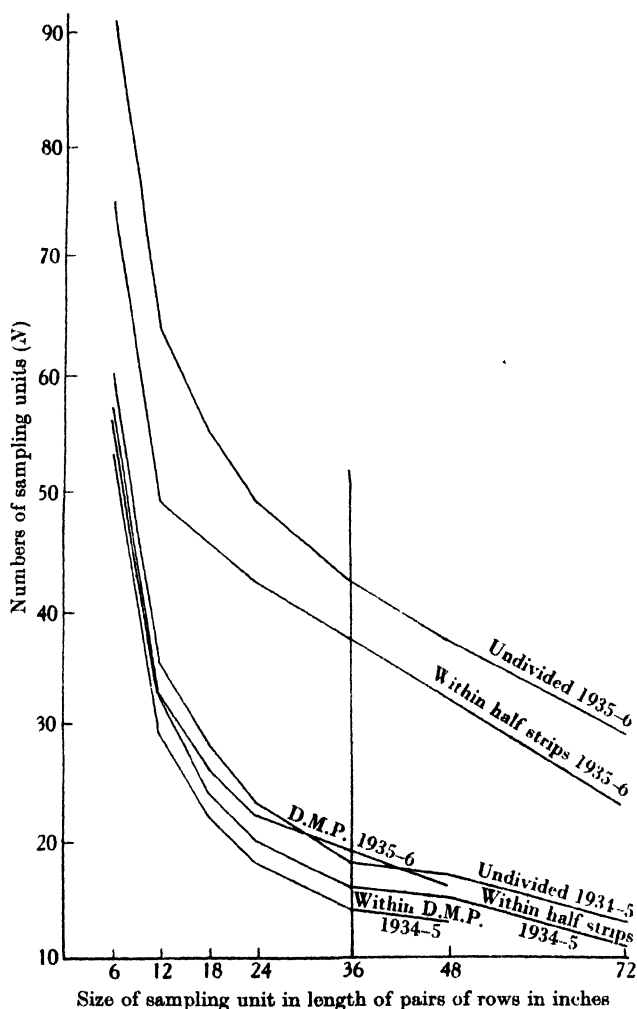


Fig. 15. Graphs of $N \times n$ for various subdivisions of strips. To show the amount of sampling necessary to obtain a 5% sampling error from plots the size of strips (1/97 acre).

Table VIII sampling errors for grain weight are given for certain randomized block experiments at Cambridge, the majority of which were sampled by taking a small percentage of the plot in foot lengths. An equal number of foot lengths were, however, taken from each row

and this considerable subdivision led to low sampling errors. In this table the sampling errors that the "Greg experiment" would have yielded if sampled by the methods employed are given, and show that the 1935-6 experiment, when greatly subdivided, actually gives the lower error, and that the variation in the crop when the fertility effect has been eliminated is similar to that found in normal experimentation.

Table VIII. *Sampling errors for grain weight of certain experiments, together with comparable sampling errors given by the Greg experiment*

Exp.	Type of land	Variety	Yield (b.p.a.)	Plot size (acres)	Sampling unit	Subdivision		Sampling %	Sampling errors		
						Size	Degree		Exp.	Greg 1934-5	Greg 1935-6
1	H	Wilhelmina	45.7	1/562	12 in. single	Rows 15 ft	1/8	13.3	10.67	8.78	8.66
2	L	Squarehead's Master	26.6	1/581	14 ft. single	None	—	20.0	14.29	11.01	—
3	L	Squarehead's Master	26.6	1/581	14 ft. single	None	—	40.0	6.83	6.74	—
4	H	Holdfast	40.1	1/581	14 ft. single	None	—	20.0	9.13	11.01	—
5	H	Holdfast	40.1	1/581	14 ft. single	None	—	40.0	5.59	6.74	—
6	H	Wilhelmina	51.7	1/122	12 in. single	Rows 57 ft	1/10	5.3	6.11	7.01	5.85
7	H	Yeoman	55.4	1/155	12 in. single	Rows 30 ft.	1/15	6.7	6.13	7.02	5.72
8	H	Yeoman	38.1	1/129	12 in. single	Rows 36 ft.	1/10	5.6	7.52	7.01	5.85
9	H	Wilhelmina	53.7	1/77	18 in. \times 4 rows	1/5 plot	1/5	6.7	3.74	5.07	7.38
10	L	Barley	—	1/72	12 in. singles	Rows 60 ft	1/10	5.0	6.13	7.04	6.06
12	L	Barley	—	1/145	18 in. fives	1/4 plot	1/4	18.75	4.86	4.53	5.70

H = heavy clay; L = light gravel.

(4) *Practical test of the validity of results*

The figures given in Table VII are based on theoretical considerations, and the opportunity was taken of testing the figures in a practical way. From the experiment of 1/20 acre, consisting of 480 separate 18 in. fives, 120 samples each consisting of 20 18 in. fives were taken—giving a sample of 4.17% of the plot. These samples were drawn in groups of ten—for the first sample 20 units were drawn at random from the 480; for the second 20 were taken from the remaining 460; and for the tenth 20 were taken from the remaining 300. The error introduced by this procedure was ignored. Table VIII shows the various observations sampled, together with the mean of a sample of 20 (m), the calculated sampling error, using the method given on p. 90 (s), the expected range within which all but 5% of the samples should fall (given by $m \pm (m \times s \times 1.96)/100$), and the number of samples that actually fell outside this range in the test described above. It will be seen that the agreement between theory and practice is close.¹

¹ 18 in. fives, not 3 ft. pairs, were considered, since these calculations were made with the use of Hollerith equipment before the 1935-6 data had been investigated, and when it was thought that this shape of sampling might prove to be the optimum.

Table IX. *To show the number of samples in a population of 124 falling outside the theoretical range at the 5% point*

Observation	Year	True mean of sample of 20 18 in. fives	Calculated sampling error as % of mean	Calculated range at 5% point	No. of samples found to fall outside range. Exp. value = 6
Plant no. at germination	1934-5	2613	3.814	2418-2808	6
Plant no. at germination	1935-6	3264	3.633	3032-3496	3
Plant no. at harvest	1935-6	2663	3.289	2491-2835	9
Stem no.	1934-5	6039	4.142	5551-6527	6
Grain wt.	1935-6	2082.9	8.916	1731.8-2434.0	5
Grain wt.	1934-5	2183.1	5.668	1940.6-2425.6	5

Number of samples = 124.

(5) *Sampling of the grain/total produce ratio*

It is not always practicable to estimate yields either by full harvesting or direct sampling for grain weight, especially on experiments on "outside farms" where the problem of transport to the field station for threshing is important. Recently it has been found that the amount of sampling necessary to estimate the ratio of grain to total produce is very small, and the practice has grown of weighing the total produce from the *entire* plot, taking a small sample back to the field station, obtaining ratio of grain to total produce ratio from this small sample, and working out the yield for each whole plot by multiplying these two observations together. It is the purpose of this section to show the amount of sampling necessary to obtain a satisfactory estimate of the ratio g/t .

The data was treated in the way described for grain weight on pp. 85, 86, except that $\sigma^2 g/t$ was not obtained by the laborious process calculating g/t for each unit and squaring the values so obtained, but by using the formula

$$\begin{aligned}\frac{v_{g/t}}{(\bar{g}/\bar{t})^2} &= \frac{1}{\bar{g}^2} \cdot v_g + \frac{1}{\bar{t}^2} \cdot v_t - \frac{2}{\bar{g}\bar{t}} \text{cov } gt \\ &= \frac{1}{\bar{g}^2} \cdot v_g + \frac{1}{(\bar{g} + \bar{h})^2} \cdot (v_g + v_h + 2 \text{cov } gh) - \frac{2}{\bar{g}\bar{t}} (v_g + \text{cov } gh).\end{aligned}$$

where \bar{g} , \bar{h} and \bar{t} are the means of grain weight, straw weight and total produce respectively, v_g represents the variance of g , etc., and $\text{cov } gt$ the covariance of g and t , etc.

When the standard error is plotted against the size of sampling unit the relative positions of the lines for singles, pairs, fives and tens are similar to those for grain weight in the same year (Fig. 6), but the differences between the standard errors for sampling units of the same

size but different shape are so small that they are of no practical importance. F was calculated in the normal way and is given in Table IX for various sizes of sampling unit, together with r_{gh} , the correlation coefficient between grain weight and straw weight.

It is obvious that the sampling percentage must be governed to some extent by the value of r_{gh} . If the correlation is very high it means that grain weight and straw weight vary in a similar manner, and therefore the ratio g/h (and thus g/t) will not fluctuate greatly. In such circumstances the variance of the ratio will be small, which, in its turn, makes the sampling requirement small. This fact is expressed in the approximate relationship

$$\sigma_{g/t}^2 = 2 \left(\frac{\bar{g}}{\bar{t}} \right)^2 \left(\frac{\bar{h}}{\bar{t}} \right)^2 V_g^2 (1 - r_{gh}), \quad \dots\dots(1)$$

where V_g is the coefficient of variation of $g = \sigma_g^2/\bar{g}$. The relationship may also be written

$$F_{g/t} = 2F_g \left(\frac{\bar{h}}{\bar{t}} \right)^2 (1 - r_{gh}) \left\{ \frac{100}{100 - F_g} \right\}, \quad \dots\dots(2)$$

where F_g and $F_{g/t}$ represent the sampling percentages of g and g/t respectively. Two approximations occur in deriving these formulae: in deriving (1) it is assumed that $V_g = V_h = V_t$, and in deriving (2) that $100/(100 - k\sigma_g^2)$ (k being defined on p. 90 as $100 (m^2 h s^2)$) is unity. The formula is also approximate because \bar{g} , \bar{t} , V_g , V_t etc., all refer to an infinite population, of which the numbers used are themselves samples. Comparisons of values calculated directly and by this formulae show that the loss due to these approximations is negligible.

Table X. *Showing F for the grain: total produce ratio in 1934-5 and 1935-6 for various sizes of sampling units, together with r_{gh} , the correlation coefficient between grain weight and straw weight, and the percentage of grain*

Nature of sampling unit	No of ft. of drill row	1934-5		1935-6	
		r_{gh}	F	r_{gh}	F
6 ft. \times 10 drill rows (approx. 1 sheaf)	60	0.971	0.55	0.928	5.18
6 ft. pairs	12	0.952	0.27	0.913	1.35
4 ft. pairs	8	0.917	0.36	0.906	1.05
3 ft. pairs	6	0.915	0.34	0.900	0.88
2 ft. pairs	4	0.914	0.23	0.890	0.67
18 in. pairs	3	0.890	0.25	0.893	0.51
12 in. pairs	2	0.888	0.21	0.868	0.46
6 in. pairs	1	0.905	0.14	0.848	0.36
Percentage of grain (g/t)		37.69		35.30	

The effect on the sampling percentage of variations in r_{gh} and of percentage grain is shown in Table XI, which has been constructed by direct substitution in equation (2), and shows the amount of sampling of the grain/total produce ratio necessary to give a sampling error identical to that given by sampling 5% of the plot for grain weight direct. The saving in sampling amounts to at least 50% and may be as high as 95% if r_{gh} is high.

Table XI. *Sampling of the grain/total produce ratio*

Percentage of the plot that must be sampled to give a sampling error for the ratio g/t similar to that obtained by sampling 5% of the plot direct for grain weight. For various values of r_{gh} and percentage of grain.

Grain %	r_{gh}						
	0.5	0.75	0.80	0.85	0.90	0.95	0.98
50	1.31	0.66	0.52	0.39	0.26	0.13	0.05
33	2.31	1.15	1.93	0.69	0.46	0.23	0.09
25	2.94	1.47	1.18	0.88	0.59	0.29	0.12
20	3.37	1.69	1.35	1.01	0.67	0.34	0.13
15	3.79	1.90	1.51	1.14	0.76	0.38	0.15
10	4.76	2.13	1.70	1.28	0.85	0.43	0.17

It is felt that the correlations in these two experiments are high, and that little confidence can be placed in the very low sampling percentages which result, but there is no doubt that there is a great reduction in the amount of labour when this method is used. If some suitable method of taking samples can be worked out this method may well prove more satisfactory than direct sampling even on experimental farms with threshing equipment at hand. It has, however, two disadvantages: first, that it is impracticable to use it in any scheme where developmental counts are being made, and secondly, that, should the straw weight be required, two weighings are necessary. This second problem, which has been discussed by Yates & Zacopanay (1935), arises because the rate of drying of grain and straw may differ. The ratio by which the total weight of produce in the field at harvest must be multiplied to give the total weight of threshed grain is

$$\frac{\text{weight of grain at threshing}}{\text{total weight of sample in field}} = \frac{g}{t}$$

and to give the total weight of straw is

$$\frac{\text{total weight of sample at threshing} - \text{grain weight at threshing}}{\text{total weight of sample in field}} = \frac{h}{t}$$

These two fractions will not account for the whole weight of produce from each plot, the fraction $(1 - g/t - h/t)$ being the amount lost by

drying. The sample must be weighed both in the field and at threshing if both g/t and h/t are required, but only in the field if h/t is not required.

The samples in the experiments described were not weighed in the field at harvest, the total weight being the sum of grain weight and straw weight at threshing. This has the effect of making the ratios g/t and h/t too large.

(6) *The formation of a sampling programme*

It has been shown that, in order to control the sampling error with any accuracy both the size of plot and the degree of subdivision must be studied. The size of the sampling unit is also important, and provided that about 6 ft. of drill row is incorporated the actual shape appears to be of secondary importance. There is, however, evidence to show that the optimum shape is 3 ft. of two adjacent drill rows and that extremes of length or width are undesirable.

The most important principle of sampling is to subdivide as much as possible. In order to fulfil the condition that an equal number of sampling units must be taken from each subdivision it frequently happens that more sampling units than theory demands have to be taken, and there is the danger that, if there are many subdivisions, this excess will make the subdivision unprofitable. In practice it is rarely worth having more than ten subdivisions unless a very small sampling unit is chosen or the plot is very large.

In forming a sampling programme the first step is to determine the approximate number of sampling units per plot required, in order that a suitable degree of subdivision may be fixed; the number will, of course, depend on the size of the plot. It has been assumed that the values obtained for grain weight in 1934-5 give degrees of sampling which will give sufficient accuracy for all observations in the majority of cases, and that values of the number of sampling units which will give a sampling error of about 5% may be looked up in Table VII.

Having determined the degree of subdivision it is necessary to decide how to divide. If possible each coulter should be sampled equally—a device that will allow for faulty coulter—-and when sampling units of 3 ft. pairs are used this is done by subdividing into pairs or rows running the length of the plot. When this is not possible little is lost by dividing into half-drill widths and taking sampling units of 18 in. fives.

As an example, let us determine the best method of sampling plots 122 ft. long and two drill widths of twelve coulter wide, with discards

of 1 ft. at each end and two drill rows on each side, so as to obtain a sampling error of 5%. The size of plot is 1/26 acre. From Table VIIb the number of sampling units necessary with subdivision is about 20. In this case ten subdivisions may be made, and two sampling units taken from each subdivision. Turning to the plot, a very convenient form of subdivision is into pairs of rows running the length of the plot, as this will ensure that each coulter row is sampled to the same extent. Two sampling units will be taken from each subdivision, making twenty sampling units in all, and 5% of the plot.

The sampling would have been very different if the length of plot had been only 32 ft., giving a plot size of 1/116 acre. About fourteen sampling units would be required, and the plot would be best sampled by dividing into four subdivisions of five rows \times 30 ft., and taking three sampling units of 18 in. fives from each—twelve¹ sampling units in all, representing 15% of the plot. This may be compared to the inferior procedure of dividing into ten subdivisions of two rows \times 30 ft. and taking two sampling units of 3 ft. pairs from each—twenty sampling units in all, representing 20% of the plot.

SUMMARY

The design and field technique of two large scale experiments, laid down to investigate the problems of sampling and “propinquity”, are described in detail. These experiments were designed so that the plant number, stem number, ear number, straw weight and grain weight for 7200 lengths of 6 in. of drill row, together with the position of each observation, might be obtained.

The lowest sampling error, expressed as a percentage of the mean, is obtained by using the smallest sampling unit, but the large number of sampling units of this size that would have to be taken make it impracticable. The optimum sampling unit consists of 6 ft. of drill row, taken as 3 ft. of two adjacent rows. The size of the sampling unit is of greater importance than the shape in determining its accuracy, and little is lost by using sampling units of 18 in. of five adjacent rows.

The nature of the observation affects the degree of sampling. In the experiments examined the plant number, stem number and ear number require very similar sampling, but grain weight requires a sample which is about twice as large as that required by the other observations.

¹ Taking advantage of the fact that since 18 in. fives are slightly larger than 3 ft. pairs, the number of them required will be slightly less.

The percentage of the plot that must be taken as a sample (the sampling percentage) to obtain any given accuracy is related to the size of plot: the larger the plot, the lower the sampling percentage necessary. To obtain an error of 5 % of the mean the sampling percentage for grain weight is approximately 5 % in 1/20 acre plots, 15 % in 1/100 acre plots and 43 % in 1/600 acre plots if the plots are not subdivided. These percentages are similar to those calculated from various randomized block experiments in Cambridge.

Subdividing the plot and taking equal numbers of sampling units from each subdivision increases the accuracy of sampling greatly, since large scale variation, such as fertility trends, can be eliminated. The possible variation between coulter rows of the drill may be eliminated by subdividing into pairs of rows.

The alternative of weighing the total produce and sampling for the grain/total produce ratio is considered. Low sampling errors of this ratio were found, and it is thought that this method is capable of wide application, especially for experiments laid down on "outside farms".

The actual percentage of the plot that must be taken has to be considered in relation to plot size and degree of subdivision. Considering plots one drill-width wide, with those of 1/100 acre (72 ft. long) the best procedure is to divide the plot into five parts, each part consisting of two drill rows, and to take three sampling units (of 3 ft. of two adjacent rows) from each subdivision; with those of 1/200 acre (36 ft. long), if similarly divided, sufficient accuracy would be obtained by taking samples consisting of two sampling units from each subdivision; and with those of 1/600 acre (12 ft. long) it is necessary to take a similar number, so taking 50 % of the plot. Values for various other plot sizes and degrees of subdivision are set out in Table VII on p. 100.

These results were obtained from Holdfast wheat grown on light gravel soil with a yield of about 35 bushels/acre. The variations in the crop, however, were shown to be of the same order as those encountered in various experiments sown on light gravel and heavy clay in which Yeoman, Wilhelmina, Holdfast, and Squarehead's Master were represented, and the yields varied from 26.6 to 55.4 bushels/acre.

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ALLOMETRIC GROWTH OF THE FORELIMB IN CATTLE

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(With Two Text-figures)

ANALYSING Hammond's data on the growth of limbs in the sheep, Huxley (1932) found a post-natal simple *negative* heterogony, or allometry, as in the latest terminology (Teissier, 1937), of the whole limb relative to the body. As lambs, and the young of most other grazing mammals, are born with relatively long limbs enabling them to follow their dams (Hammond, 1932), the same author pointed out that the leg must have exhibited *positive* allometry during foetal development.

Having possession of a sufficient body of measurements on the skeletal development of female calves of the Chianina breed, a very tall beef and draft breed of cattle of Central Italy, I investigated the course of growth of height at withers relative to the growth of the length of the trunk (from shoulder to ischium). The growth of height at withers can be considered as a sufficiently reliable measure of the growth of forelimb length owing to the fact that the two principal angles in the limb (scapula-humerus and humerus-radius) do not change very much with age (Engeler, 1935).

It was found that the growth of forelimb length in this breed of cattle exhibits a simple *negative* allometry relative to the growth of trunk length. This simple allometry, with *growth constant* about 0.78, holds from birth until over the age of 3 years, that is, throughout practically the whole post-natal growth.

Lack of data after this age leaves open to further research the course in the ultimate period of development.

I thought it would be of some interest to compare various breeds of cattle differing rather widely in the absolute values, as well as in the proportions of height at withers and trunk length at birth and in later life.

The data by Szabo v. Hangai (1929) on the Simmenthal and on the

Hungarian Grey breed, by Missouri investigators (1926) on the Holstein and the Jersey, by Engeler (1935) and Carusi (1929) on the Brown Swiss, and my data on the Chianina, plotted in logarithmic scale in Fig. 2, show that for individuals kept on a constant plane of nutrition the simple negative allometric growth of forelimb throughout the whole or the greatest part of post-natal development seems a general rule for the species.

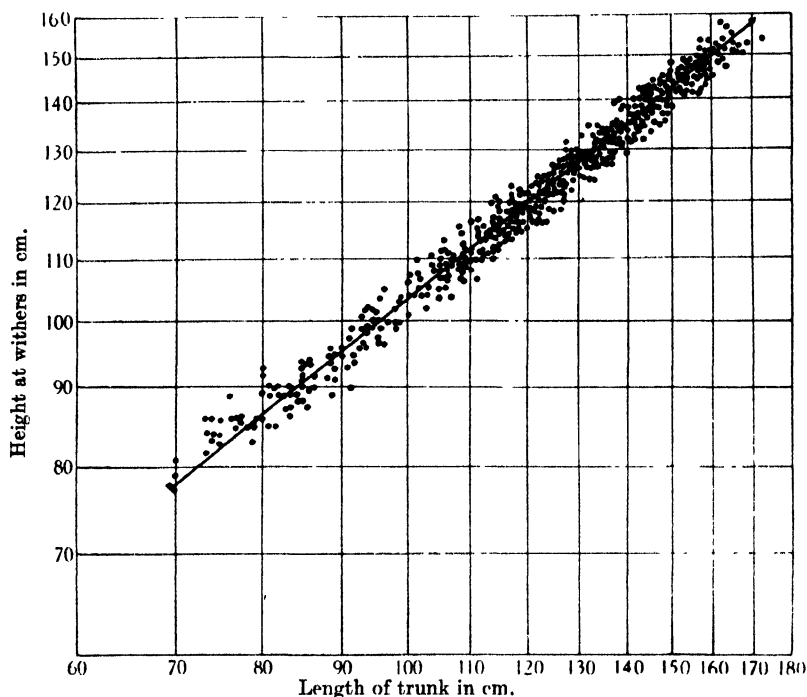


Fig. 1. Individual measurements of females of the "Chianina" breed.

Further, the following equations to the curves of Fig. 2, in the form $y = bx^\alpha$, give evidence of the fact, that with the exception of the Simmenthal breed, the *growth constants* α (or *constant differential growth ratios* as in the earlier terminology) are very close for the five other breeds. If allowance is made for different planes of nutrition and for other environmental conditions possibly acting differentially on growth, it can be argued that under identical conditions the five breeds might show the same *growth constant*. What differs rather widely between breeds is the *origin index* b , which, however, has no biological significance in this case, because the relative growth of limbs and trunk must follow, as pointed

out by Huxley, a quite opposite allometric course in the foetal and in the post-natal development.

The inversion from the foetal *positive* to the post-natal *negative* allometric growth is a matter of speculation.

Breed	Allometric equation	At birth			At 12 months			At maturity		
		H	L	L/H	H	L	L/H	H	L	L/H
Brown Swiss	$H = 3.20L^{0.742}$	72.5	63	0.87	114	122	1.07	135	163	1.21
Simmental	$H = 4.54L^{0.675}$	79.6	71.1	0.89	122	130	1.06	—	—	—
Hungarian Grey	$H = 2.90L^{0.757}$	78.7	77.2	0.98	109	121	1.12	—	—	—
Holstein	$H = 3.05L^{0.741}$	70.4	60	0.86	113	130	1.15	135	169	1.25
Jersey	$H = 2.71L^{0.761}$	66.8	64.6	0.97	106	126	1.19	126	154	1.23
Chianina	$H = 2.78L^{0.785}$	79	70	0.87	133	138	1.04	156	177	1.13

H = height at withers; L = length of trunk.

Examination of the data for all the breeds shows that the above-mentioned inversion does not occur *after* birth. It might occur *at* birth

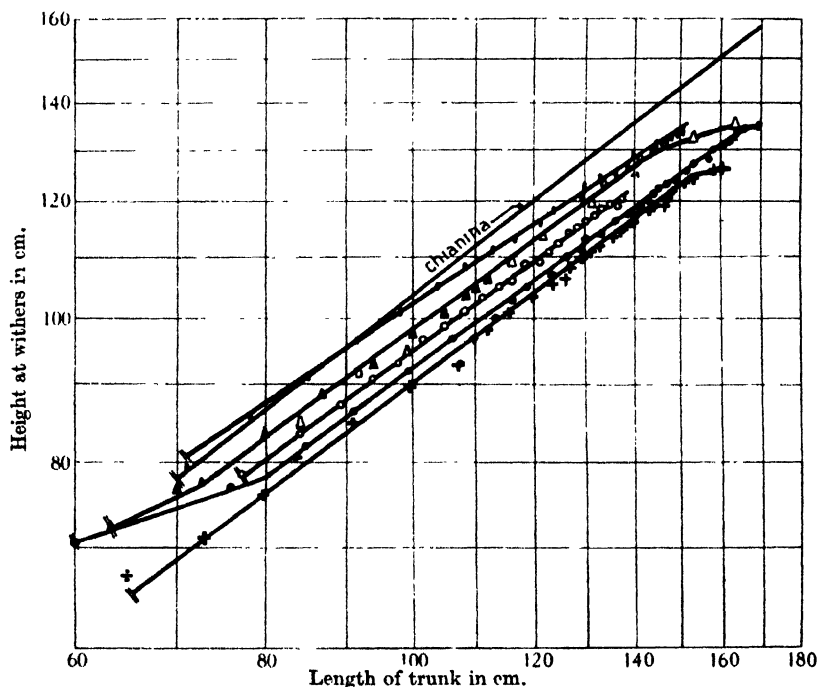


Fig. 2. Average measurements of six breeds.

- | Simmental (Szabo). ▲ Brown Swiss (Carusi) and △ (Engler).
 ○ Hungarian Grey (Szabo). ● Holstein (Missouri). + Jersey (Missouri)
 || Birth.

or *before* birth. Investigations on this problem during foetal development, following Teissier's idea of "stades critiques", would be very interesting.

For two of the breeds, the Brown Swiss and the Holstein and perhaps also for the Jersey, there is some rather doubtful evidence (Fig. 2) of a period following birth, in which there is still more marked negative allometry, as though the most rapid *relative* growth of the trunk occurred just after birth. But this evidence needs a sounder statistical basis.

In any case, as the post-natal *growth constant* shows very close values for five out of six of the breeds, the genetical differentiation probably is determined by genes acting on the foetal development and affecting (a) the *course of relative growth* of limbs and trunk length, (b) the *time* of appearance of the inversion, and (c) the *course* of the inversion, rather than by genes acting on the post-natal development.¹

It seems that the absolute value and the proportions of limb length and trunk length at the moment at which growth begins to follow the post-natal allometric law—whether this moment coincides with birth or precedes it—may play an important part in determining the subsequent developmental breed differences.

The matter seems worthy, from the point of view of breeding practice, of further investigation, as it is possible that within breeds the size and proportions of the new-born are not negligible factors in the determination of size and proportions in later development.

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¹ In a recent paper Walton & Hammond (1938), *Proc. roy. Soc. B*, **125**, 311, analysing the maternal effects on growth in Shire horse-Shetland pony crosses, reach some very interesting conclusions on the genetic differentiation of the pure- and cross-breeds. It seems worthy to point out the close agreement between the conclusions of these authors and those reached in the present paper by a quite different way and on a different species.

THE NUTRITION OF THE BACON PIG

III. THE MINIMUM LEVEL OF PROTEIN INTAKE CONSISTENT WITH QUICK GROWTH AND SATISFACTORY CARCASS QUALITY (PART I)

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INTRODUCTION

IN the first paper of this series (Woodman *et al.* 1936) a description was given of feeding trials in which a very heavy replacement of cereal by protein-rich food in the diet of bacon pigs was shown to have had only the slightest effect on the rate of live-weight increase between weaning and slaughter and to have given rise to carcasses neither leaner nor fatter than those produced from diets containing the customary amounts of protein-rich foods. It was concluded that the excess of protein beyond the actual requirements for maintenance and body-protein synthesis must have undergone deamination and have functioned, directly or indirectly, like carbohydrate in the production of body fat. The correctness of this explanation was demonstrated in a second paper, in which the results of an investigation into the influence of high-protein intake on protein and mineral metabolism in the bacon pig were described (Woodman *et al.* 1937).

In the present trial, which in part was designed to secure further information on the subject of high-protein feeding, the mixture of white fish meal, meat meal and ex. soya-bean meal used as the main supply of protein in the first trial has been replaced by a mixture of dried separated milk, feeding blood meal and ex. soya-bean meal. The present mixture differed from the previous one by having a very low content of oil, a constituent which, if present in large amount, might conceivably tend to obscure the true significance of the results of investigations in which body-fat production from food protein formed part of the problem under study.

The scope of the inquiry was also extended in the direction of investigating the consequences of depressing the level of protein supply below that usually considered necessary for satisfying the demands for protein in the rapidly growing pig. With rations composed substantially of cereals and cereal offals, the food of weaners should contain, according to the standards of modern practice, 10–12 % of white fish meal, or its equivalent in the form of other protein-rich foods, though some authorities consider as much as 20 % of fish meal, or its equivalent, to be desirable in the earliest stages of feeding. Beyond 150 lb. live weight, the amount of such protein-rich food, usually in some form other than fish meal to avoid the risk of taint, should be reduced to about 5 % of the ration.

With the object of examining the question of protein supply from a broader standpoint, therefore, one of the three feeding treatments (A) in the present trial was made up so as to supply, in the early stages of growth, an amount of protein-rich food equivalent, from the standpoint of protein content, to about $4\frac{1}{2}$ % of fish meal. The other feeding treatments (B and C) contained amounts of protein-rich food equivalent to about 9 and 18 % of fish meal respectively. The extra protein food in these treatments was introduced in replacement of barley meal, lb. for lb., and since the starch equivalents of the barley and the protein supplement were nearly equal, namely, about 70, differences in net energy supply could be ruled out as a possible explanation of any differences that might be observed in the rate of live-weight increase of the pigs on the three feeding treatments.

Since treatment B contained approximately what have come to be regarded as the standard amounts of protein-rich food, it was anticipated that growth on the low-protein treatment A, particularly in the early stages, might be markedly retarded, and that the carcasses might display a sharp distinction, in respect of fatness, from those of the pigs on the treatments with the higher protein supply. It is one of the objects of this paper to show that this expectation was not realized.

The scheme of the feeding treatments and the mean composition of the feeding stuffs used in making up the rations are given in Tables I and II. The feeding chart in Table III shows how the meal supply was scaled in relation to the live weight of the pigs.

It will not be necessary to give a detailed description of the conduct of the trial, since the procedure was identical with that adopted in the first trial of this series (Woodman *et al.* 1936). Each of the five pens of the individual-feeding lay-out contained six Large White pigs from a given litter, three hogs and three gilts. The three feeding treatments,

Table I. *Scheme of feeding experiments*

	Parts by weight ...	Low-protein treatment A	Standard-protein treatment B	High-protein treatment C
Up to 90 lb. L.W.:				
Barley meal		61	55	43
Weatings		31	31	31
Lucerne meal		2	2	2
{ Ex. soya-bean meal	}	3	6	12
{ Dried separated milk		2	4	8
{ Feeding blood meal		1	2	4
Minerals		2	2	2
*Equivalent amount of white fish meal		4.5	9	18
90-150 lb. L.W.:				
Barley meal		70	65	55
Weatings		23	23	23
Lucerne meal		2	2	2
{ Ex. soya-bean meal	}	2.5	5	10
{ Dried separated milk		1.5	3	6
{ Feeding blood meal		1.0	2	4
Minerals		2	2	2
*Equivalent amount of white fish meal		3.8	7.6	15.2
150 lb. L.W. to slaughter:				
Barley meal		82.5	80	75
Weatings		13	13	13
Lucerne meal		2	2	2
{ Ex. soya-bean meal	}	1.25	2.5	5
{ Dried separated milk		0.75	1.5	3
{ Feeding blood meal		0.50	1.0	2
Minerals		2	2	2
*Equivalent amount of white fish meal		1.9	3.8	7.6

Note. The minerals consisted of 1 part by weight of common salt to 3 parts of ground chalk.

Table II. *Average composition of feeding stuffs*

	Barley meal	Weatings	Lucerne*	Ex. soya-bean meal	Dried separated milk	Feeding blood meal
	%	%	%	%	%	%
Moisture	13.80	14.53	13.80	13.51	10.34	8.89
Crude protein	10.08	15.08	22.48	44.22	32.77	84.85
Ether extract	2.73	4.10	5.64	1.27	1.50	0.77
N-free extractives	66.35	59.99	31.92	30.15	47.91	1.44
Crude fibre	4.76	3.90	16.90	5.32	—	—
Ash	2.28	2.40	9.26	5.53	7.48	4.05
Iodine value of petrol-ether extract	120.6	128.2	128.2	111.7	43.7	60.5

* Lucerne crop cut high so as to give product very rich in leaf.

Table III. *Feeding chart**

L.W. in lb.	lb. meal	L.W. in lb.	lb. meal
20	1.10	120	5.30
40	2.10	140	5.90
60	3.00	160	6.45
80	4.00	180	6.70
100	4.60	200	7.00

* Change in meal allowance shown for live-weight increments of 20 lb.; adjustments should be made for intermediate live weights, so that the meal supply may be altered week by week in accordance with the results of the weekly weighings of the pigs.

A, B and C, were applied to the three hogs and also to the three gilts, so that each of the five pens provided two simple comparisons of the effect of the three feeding treatments in which the factor of sex was also taken into account. The design of the experiment is shown in Table IV. In addition to the individual-feeding trial, three groups of ten Large White pigs were formed for the purpose of comparing the effects of the feeding treatments by the group-feeding technique. The customary precautions were observed in making up these groups.

The distribution of the pigs into pens and groups was carried out on

Table IV. *Live-weights gains and meal consumption of individually-fed pigs over period of 16 weeks (17 September 1935-7 January 1936)*

Feeding treatment	No. and sex of pig	Weaning L.W. lb.	L.W. on 17 Sept. lb.	L.W. on 7 Jan. lb.	Total meal consumed lb.
Pen I (sow 237)*					
A	G 1291	30	48½	206	531.35
B	G 1289	33½	50	203½	554.75
C	G 1290	37	61	222	604.45
C	H 1294	28	44½	186½	512.40
B	H 1292	25	44	196	512.45
A	H 1285	30½	46	193½	514.95
Pen II (sow 451)*					
B	G 1318	26	30	164	415.25
C	G 1320	28	35	161	439.25
A	G 1321	26	31½	162	421.30
C	H 1317	27	32½	175½	452.10
A	H 1313	28	33½	157½	415.65
B	H 1316	37	45	204	537.95
Pen III (sow 434)*					
C	G 1362	26½	34	187	484.75
A	G 1363	33	37½	173	459.95
B	G 1361	34	40½	186½	495.85
B	H 1357	40	47	193	527.60
C	H 1358	40½	49	196	536.70
A	H 1360	41½	49	197½	527.65
Pen IV (sow 333)*					
C	G 1296	37	49	188	517.70
A	G 1303	37	46	194	525.15
B	G 1299	39	50	205	544.75
A	H 1300	31	43	194	503.05
B	H 1297	33	45	192	526.75
C	H 1302	35	48	211	542.35
Pen V (sow 447)†					
B	G 1355	26	30	158½	423.85
A	G 1345	26½	29	161	410.90
C	G 1344	34½	38	189½	499.40
B	H 1351	36	42	173	493.85
C	H 1348	35½	41	186	513.45
A	H 1352	37	39½	175	479.50

* Sire: "Davidson".

† Sire: "Buttercup".

the basis of their live weights on 3 September 1935. The animals were brought on to their respective rations for the experiment on 10 September. They were weighed again on the mornings of 16, 17 and 18 September, and the means of these three weighings were taken as the initial weights in the trial.

PRE-SLAUGHTER RESULTS

Table IV, in addition to showing the lay-out of the individual-feeding trial, also gives the initial live weights and the food consumption of the individually-fed pigs together with their live weights on 7 January, on which date the comparison of the influence of the feeding treatments on live-weight increase was discontinued as a consequence of the dispatch of the first consignment of pigs to the bacon factory. Full records for both the individually-fed and group-fed pigs were still kept, however, until every animal had reached 200 lb. live weight.

In Table V are recorded the average live weights, as determined week by week, of the pigs under the three feeding treatments. It is not feasible, from considerations of space, to tabulate all the intermediate weekly

Table V. *Average weekly live-weights of pigs under different feeding treatments*

Treatment ...	Individually-fed pigs			Group-fed pigs		
	A lb.	B lb.	C lb.	A lb.	B lb.	C lb.
17 Sept.	40.35	42.35	43.20	41.25	41.75	42.30
24 "	44.90	47.40	49.15	45.05	46.85	47.20
1 Oct.	51.25	54.70	56.90	50.80	53.10	54.45
8 "	57.30	61.80	64.50	56.35	59.50	62.15
15 "	65.20	70.75	72.90	63.15	66.80	70.30
22 "	72.50	79.05	81.30	70.95	74.80	77.10
29 "	78.95	86.15	88.80	76.60	81.70	83.65
5 Nov.	88.30	95.10	98.80	84.70	88.95	92.55
12 "	95.95	103.35	106.35	92.85	97.90	100.45
19 "	105.40	112.75	115.80	102.45	106.00	109.70
26 "	115.20	122.95	125.00	111.10	114.40	118.65
3 Dec.	124.25	133.45	135.45	119.55	125.65	128.35
10 "	135.40	144.40	146.90	130.05	134.35	138.15
17 "	146.55	153.70	156.60	140.95	144.80	147.65
24 "	158.15	165.00	168.20	152.15	153.95	158.60
31 "	169.90	176.10	179.30	163.20	165.95	168.00
7 Jan.	181.35	187.55	190.25	172.55	174.30	176.80

Total meal consumed from 17 September to 7 January

	Individually-fed pigs lb.	Group-fed pigs lb.
By 10 A pigs	4789.45	4742.15
By 10 B pigs	5033.05	4882.25
By 10 C pigs	5102.55	4980.50

weights of the separate animals in the experiments. It is sufficient to note that the trial as a whole proceeded satisfactorily from the standpoint of the health of the pigs, and that there were no cases of mishap or serious disturbance.

Comments on Tables IV and V

Individual-feeding results. The results in Table V for the individually-fed pigs over the whole period of comparison show a small but consistent rise in passing from treatment A to treatment C. The observed differences, however, have no statistical significance, the essential figures being:

	A	B	C	Mean	S.E.
Average L.W.I. over period (lb.)	141.0	145.2	147.0	144.4	2.96

The correlation of live-weight increase with amount of meal consumed is significant ($b=0.1912$, $r=+0.698$). If the results are corrected for differences in meal consumption, the small differences in live-weight increase on the three treatments disappear almost entirely. The figures now become:

	A	B	C	Mean	S.E.
Average L.W.I. adjusted for meal consumed (lb.)	144.6	144.1	144.6	144.4	2.18

The standard error of each pig's live-weight increase is 9.4 lb., i.e. 6.5 % of the mean live-weight increase of all the pigs in the individual-feeding trial.

It may be concluded that the effect of feeding treatment on live-weight increase was not significant. The results are analysed in greater detail in Table VI in order to discover whether the treatments had produced any significant differences in the rate of growth at any particular stage of the feeding period.

Table VI. *Analysis of results for individually-fed pigs (averages of results for 10 pigs in each treatment)*

Treatment	L.W. on 17 Sept. lb.	Up to 90 lb. L.W.			90-150 lb. L.W.			150-200 lb. L.W.			Whole trial		
		No. of days re-quired	lb. L.W.I. per day	lb. meal per lb. L.W.I.	No. of days re-quired	lb. L.W.I. per day	lb. meal per lb. L.W.I.	No. of days re-quired	lb. L.W.I. per day	lb. meal per lb. L.W.I.	No. of days on exp.	lb. L.W.I. per day	lb. meal per lb. L.W.I.
A	40.35	51.1	0.99	2.96	42.3	1.43	3.53	30.3	1.66	3.97	123.7	1.30	3.49
B	42.35	45.0	1.08	2.78	42.8	1.40	3.58	33.4	1.50	4.35	121.2	1.31	3.58
C	43.20	42.6	1.12	2.70	43.8	1.38	3.65	32.5	1.55	4.24	118.9	1.33	3.56
S.E.			0.024	0.061		0.029	0.069		0.042	0.113		0.022	0.067
Treatment effect			S.S.	S.		N.S.	N.S.		N.S.	N.S.		N.S.	N.S.
			B < A	A < B									

S.=significant at 5 % point. S.S.=significant at 1 % point. N.S.=not significant.

Comments on Table VI

The figures in Table VI show that although the feeding treatments produced no significant differences in the rate of live-weight increase and in the efficiency of food conversion when the trial is considered as a whole, yet in the initial period of growth up to 90 lb. live weight, the pigs on the low-protein diet A made slightly but significantly smaller live-weight gains than the pigs on treatments B and C. At this stage the difference in respect of rate of live-weight increase is significant at the 1 % point, whilst the slight difference in favour of the B and C pigs in regard to the efficiency of food conversion is significant at the 5 % point.

The differences are still significant if the results are adjusted for differences in the initial live weights of the pigs in the three treatments. If, however, the adjustment of the results for the period up to 90 lb. live weight is made to an initial live-weight of 60 lb. (which, of course, is considerably higher than the actual initial live weights—see Table VI) then the differences both in respect of rate of live-weight increase and efficiency of food conversion, though still discernible, are no longer statistically significant, the relevant figures being:

	A	B	C	Mean	S.E.
From 60–90 lb. L.W.:					
Average lb. L.W.I. per day	1.13	1.20	1.20	1.18	0.029
Average lb. meal per lb. L.W.I.	3.06	2.89	2.87	2.94	0.074

From this it may be inferred that only in the earliest stage of the trial, during the period following weaning up to about 60 lb. live weight, was the slightly slower rate of growth of the A pigs statistically significant, and that significant differences in growth rate arising from the low protein supply in treatment A had ceased to be manifested beyond 60 lb. live weight. Since over the whole period up to 200 lb. live weight there were no significant differences attributable to feeding treatment in regard to rate of live-weight increase and efficiency of food conversion, it follows that the slight initial set-back experienced by the low-protein pigs must have been made up at a later stage. It will be seen from Table VI that this actually took place in the period from 150–200 lb. live weight.

The analysis of variance revealed no significant influence of sex on the rate of live-weight increase and on the efficiency of food conversion. The close agreement between hogs and gilts is also shown by the following figures for the period 60–200 lb. live weight.

	No. of days required	lb. L.W.I. per day	lb. meal per lb. L.W.I.
Mean for 15 hogs	101.4	1.39	3.67
Mean for 15 gilts	100.5	1.40	3.65

Group-feeding results. It will be seen from Table V that the average live-weight gains over the 16 weeks' period of feeding, though smaller than for the individually-fed pigs, show the same slight rise from treatment A to treatment C. As with the results for the individually-fed animals, however, the observed small differences are not significant. The essential figures are:

	A	B	C	Mean	S.E.
Average L.W.I. over period (lb.)	131.3	132.55	134.5	132.8	4.22

From the analysis of variance it is found that the standard error of each pig's live-weight increase is 13.35 lb., i.e. 10.1 % of the mean live-weight increase of all the group-fed pigs. The corresponding figure for the individually-fed pigs was 6.5 %, and since precision is measured in terms of variance, or the square of the standard error, it follows that the results for the individually-fed pigs are about $2\frac{1}{2}$ times as accurate as those for the group-fed pigs.

That the group-fed pigs gave results in general agreement with those for the individually-fed pigs is also clear from the comparisons in

Table VII. *Mean rates of live-weight increase and food conversion factors*

Treatment	Range of L.W.I. lb.	Days required	lb. meal consumed by 10 pigs	Mean lb. L.W.I. per day	Mean lb. meal per lb. L.W.I.
Individually-fed pigs					
A	40.35-90	51	1492.70	0.97	3.01
B	42.35-90	45	1356.13	1.06	2.85
C	43.20-90	43	1286.70	1.09	2.75
A	90-150	42	2101.76	1.43	3.50
B	90-150	43	2152.14	1.40	3.59
C	90-150	43	2154.19	1.40	3.59
A	150-181.35	19	1194.99	1.65	3.81
B	150-187.55	24	1524.78	1.56	4.06
C	150-190.25	26	1661.66	1.55	4.13
A	40.35-181.35	112	4789.45	1.26	3.40
B	42.35-187.55	112	5035.05	1.30	3.47
C	43.20-190.25	112	5102.55	1.31	3.47
Group-fed pigs					
A	41.25-90	53	1583.30	0.92	3.25
B	41.75-90	50	1514.05	0.97	3.14
C	42.30-90	48	1479.80	0.99	3.10
A	90-150	44	2221.55	1.36	3.70
B	90-150	44	2226.20	1.36	3.71
C	90-150	44	2241.20	1.36	3.74
A	150-172.55	15	937.30	1.50	4.16
B	150-174.30	18	1142.00	1.35	4.70
C	150-176.80	20	1259.50	1.34	4.70
A	41.25-172.55	112	4742.15	1.17	3.61
B	41.75-174.30	112	4882.25	1.18	3.68
C	42.30-176.80	112	4980.50	1.20	3.70

Table VII, in which the data from both forms of experimentation are accorded similar treatment, i.e. the number of days required for reaching 90 and 150 lb. live weight is reckoned by the dates on which the *average* weights of the pigs under the different treatments reached these values.

Comments on Table VII

The group-feeding results in Table VII show very clearly the same general features as the results for the individually-fed pigs and support the conclusion that the differences in feeding treatment had been without effect on the rate of live-weight increase and the efficiency of food conversion over the experiment as a whole, but that during the early period up to 90 lb. live weight the low protein supply of treatment A led to a slightly slower rate of growth than was manifested by the pigs on treatments B and C. As with the individually-fed pigs, however, this initial setback was made up in the later stages of the feeding trial.

It will be noted that the pigs fed as individuals displayed a higher rate of live-weight increase and required less meal per lb. live-weight increase than the pigs fed as groups. The reasons for this greater thriftiness of the individually-fed pigs, and the significance of the finding in practical feeding, have been discussed in the first publication of this series (Woodman *et al.* 1936).

POST-SLAUGHTER RESULTS

The reader is referred to the first paper of this series (1936) for a detailed explanation of the technique of the post-slaughter work. It is not proposed to record in this paper all the measurements made on the sixty carcasses, but merely to give the averages for the pigs under the three feeding treatments together with the standard errors. It should be pointed out, however, that in every case an analysis of variance was carried out in order to ascertain the significance of the effect, if any, of feeding treatment, sex and litter. Only the effect of feeding treatment will be examined in this paper. Questions relating to the influence of sex on the post-slaughter measurements will be dealt with in a future publication, in which a large number of observations accumulated in this series of trials will be submitted to statistical analysis. The following symbols are used to denote the effect of feeding treatment: N.S. (not significant), S. (significant at 5 % point), S.S. (significant at 1 % point).

Table VIII. *Effect of feeding treatment on thickness of back fat and belly streak (treatment averages)*

Treatment	Back fat*			Belly streak†			
	Max. cm.	Min. cm.	Mean cm.	(a) cm.	(b) cm.	(c) cm.	Mean cm.
(1) Individually-fed pigs							
A (10 pigs)	5.07	2.75	3.91	3.23	4.27	4.55	4.02
B (10 pigs)	5.17	2.72	3.94	3.32	4.12	4.26	3.90
C (10 pigs)	4.80	2.41	3.61	3.19	3.96	4.18	3.78
S.E. of means	—	—	0.105	—	—	—	0.09
Treatment effect	—	—	N.S.	—	—	—	N.S.
(2) Group-fed pigs							
A (10 pigs)	4.94	2.61	3.78	2.99	3.88	4.26	3.71
B (10 pigs)	4.92	2.61	3.77	3.15	3.82	4.12	3.70
C (10 pigs)	4.62	2.56	3.59	3.12	3.88	4.34	3.78

* As measured at thickest point at shoulder and thinnest point along back.

† As measured (a) opposite curve, (b) opposite junction of fourth and fifth vertebrae from curve, (c) at a distance below (b) equal to distance from (a) to (b).

Comments on Table VIII

There is a distinct suggestion in the results for the individually-fed pigs that the animals on treatment C, with its excessive protein supply, gave carcasses with a thinner back fat and belly streak than was the case with the B and A pigs. The differences, however, were small and did not reach statistical significance. What is quite clear, however, is that the very slight differences in these respects between the pigs on the standard-protein treatment B and the low-protein treatment A were entirely without significance, an entire absence of treatment effect amply borne out by the corresponding results for the group-fed animals.

Table IX. *Influence of feeding treatment on size and leanness of typical rashers (treatment averages)*

Treatment	Mean "warm" carcass weight lb.	Belly rasher*			Mid-back rasher*			Complete rasher*		
		Total area† sq. cm.	Area of		Total area† sq. cm.	Area of		Total area† sq. cm.	Area of	
			Lean sq. cm.	Fat sq. cm.		Lean sq. cm.	Fat sq. cm.		Lean sq. cm.	Fat sq. cm.
(1) Individually-fed pigs										
A (10 pigs)	161.8	90.78	29.03	59.17	132.85	42.22	88.46	223.63	71.25	147.63
B (10 pigs)	161.2	89.79	30.17	56.95	127.88	42.31	83.48	217.67	72.51	140.43
C (10 pigs)	162.0	89.36	31.23	55.18	123.73	42.40	78.53	213.09	73.63	133.71
S.E. of means			1.35	1.96		1.48	2.91		2.54	4.50
Treatment effect			N.S.	N.S.		N.S.	N.S.		N.S.	N.S.
(2) Group-fed pigs										
A (10 pigs)	161.4	92.99	27.64	62.03	126.22	42.05	81.98	219.21	69.69	144.01
B (10 pigs)	159.5	90.28	27.24	60.66	125.97	42.84	81.10	216.25	70.08	141.76
C (10 pigs)	160.5	90.19	27.17	60.51	122.79	40.96	79.64	212.98	68.13	140.15

* See first publication in this series (Woodman *et al.* 1936) for explanation of these terms.

† Total area minus sum of areas of lean and fat equals area occupied by bone.

Comments on Table IX

The results for the individually-fed pigs reveal a tendency for the low-protein treatment A to give rise to a larger, and the high-protein treatment C to a smaller complete rasher than the standard-protein treatment B. The differences in total area are not traceable to differences in the size of the belly rasher but to differences affecting the mid-back rasher only; nor are the differences to be ascribed to differences in the amount of lean deposited, since although there is a tendency for the amount of lean to increase with increasing protein supply, the differences in this respect are so very slight as to be entirely without significance.

There are, however, differences in the amount of fat in the typical rashers from the three treatments, the fat showing a tendency to rise with decreasing protein supply. These differences are more pronounced in the mid-back than in the belly rasher. If treatment B, with its standard-protein supply, be regarded as the control, the differences in this respect between the low-protein and the standard-protein treatments, as well as those between the high-protein and the standard-protein treatments, are not significant. If, however, the comparison be made between the extreme treatments A and C (low-protein and high-protein treatments), the differences in the mean amounts of fat deposited in the mid-back and the complete rashers almost reach the border-line of significance.

The actual practical significance of this difference between the extreme treatments A and C would be small. A consideration of the detailed results shows that the ranges of variation in the area of fat in the complete rasher were 118-178 sq. cm. for treatment A, 120.3-154.3 sq. cm. for treatment B and 109.9-175.7 sq. cm. for treatment C. Clearly the variation within any one treatment was much greater than the difference between the averages for the extreme treatments A and C. Further, if the fat be expressed as a percentage of the total rasher, the influence of feeding treatment is found to be without significance. The averages of these percentages for the three treatments are:

	A	B	C	S.E.
Fat as % of total rasher	65.87	64.50	62.54	1.29

The corresponding values for the group-fed pigs show a high degree of agreement, viz. 65.61, 65.48 and 65.66% for treatments A, B and C respectively. It will be noted from Table IX that the group-feeding results, whilst in general qualitative agreement with those for the individually-fed pigs, show much smaller increments in the amount of

fat in the typical rashers as a result of decreasing the protein supply in the ration.

Table X. *Influence of feeding treatment on "eye" muscle measurements (treatment averages)*

Treatment	Space within line of connective tissue			“Eye” muscle		Back fat opposite “eye” cm.
	Total area	Area of lean	Area of fat	Length cm.	Depth cm.	
	sq. cm.	sq. cm.	sq. cm.			
(1) Individually-fed pigs						
A (10 pigs)	35.01	30.34	4.67	7.90	5.74	2.98
B (10 pigs)	34.93	30.06	4.87	7.87	5.48	2.92
C (10 pigs)	36.10	30.95	5.15	8.00	5.84	2.76
s.e. of means	0.91	1.02	0.55	—	—	0.15
Treatment effect	N.S.	N.S.	N.S.	—	—	N.S.
(2) Group-fed pigs						
A (10 pigs)	35.90	30.75	5.24	7.53	6.16	2.78
B (10 pigs)	36.08	30.47	5.61	7.75	5.86	2.79
C (10 pigs)	36.09	30.36	5.73	7.82	5.76	2.75

Comments on Table X

Both the individual-feeding and the group-feeding results afford very conclusive evidence that the dimensional characteristics of the important "eye" muscle, which may be regarded as an index of muscular development, were not affected by the differences in the level of protein supply in the three feeding treatments. The individual-feeding results demonstrate the non-significance of the small differences between the treatment averages for the area within the line of connective tissue, the actual amount of lean muscle and the extent of fat infiltration. The treatment averages for the thickness of back fat opposite the "eye" muscle also show no significant differences.

The range of variation in the averages for the area of lean muscle was exceedingly restricted, being merely from 30.06 to 30.95 sq. cm. This remarkably close agreement for all the treatments in both the group-feeding and individual-feeding trials suggests that all the feeding treatments, including treatment A with its low protein supply, supplied sufficient protein to enable the development of the "eye" muscle to be carried to its natural limit.

Comments on Table XI

Certain conclusions can be drawn without difficulty from the results for the individually-fed pigs. The treatment averages for the "warm" carcass percentage, length of middle, weight of sides as percentage of

Table XI. *Influence of feeding treatment on certain post-slaughter measurements (treatment averages)*

Treatment	L.W. at factory* lb.	“ Warm ” carcass per- centage†	Length of middle‡ cm.	Flares§ gm.	Kidneys§ gm.	Fillet§ gm.	Sides as % of carcass weight	Fillet§		Iodine value of back fat¶
								% fat	Iodine value of fat	
(1) Individually-fed pigs										
A (10 pigs)	200.1	80.86	78.09	1662.9	240.3	671.7	77.31	1.65	67.88	63.55
B (10 pigs)	196.8	81.89	77.52	1549.0	256.1	732.9	77.09	1.68	67.74	64.02
C (10 pigs)	199.4	81.24	79.38	1451.9	259.8	780.1	77.04	1.48	67.09	63.79
s.e. of means		0.35	0.56	60.82	5.77	40.89	0.28	0.10	0.88	0.50
Treatment effect		N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
(2) Group-fed pigs										
A (10 pigs)	200.5	80.53	78.12	1627.3	240.6	651.3	77.52	1.61	65.07	63.30
B (10 pigs)	197.2	80.87	77.64	1670.4	252.1	701.9	77.51	1.58	63.48	63.54
C (10 pigs)	199.9	80.27	79.13	1447.4	262.6	708.9	77.46	1.54	65.08	62.98

* After 24 hr. fast and road transport of about 40 miles to factory.

† Without applying the allowance for shrinkage on cooling.

‡ As measured from front rib to pubis symphysis.

§ Total weights of flares, kidneys and fillets from both sides.

|| Based on weights of trimmed sides before curing.

¶ Back fat sampled from gammon end of sides.

carcass weight and percentage of fat in fillets show no significant differences; the group-feeding results, moreover, are entirely in harmony with these findings.

There is, however, a distinct tendency for the weight of the flares to increase with decreasing protein supply; indeed, the difference between the means for the extreme treatments A and C comes very close to actual significance. Since the general fatness of the carcass is frequently, but by no means invariably, associated with high flare weight, it might be thought that the results for the flares should be taken as suggesting that the decrease in protein supply from treatment C to treatment A had led to an increase in the general fatness of the pigs, but this inference would not be in accord with the findings already discussed. It is important to note that if treatment B be taken as the control, then there are certainly no significant differences in respect of flare weight between the standard-protein and low-protein treatments on the one hand, and the standard-protein and high-protein treatments on the other. Moreover, the group-feeding results do not reveal any tendency for the low-protein pigs to produce heavier flares than the standard-protein animals. In all cases, the range of variation of flare weight within any one treatment was very much greater than the extreme difference between the means for treatments A and C.

The treatment averages for the weights of the kidneys give rise to considerations of a similar nature. There is a distinct tendency for kidney

weight to rise with increasing protein supply, and the difference between the means for the extreme treatments A and C comes near to actual significance, a finding in agreement with the result given in this regard in the first paper of this series (Woodman *et al.* 1936). It need scarcely be pointed out, of course, that since the kidneys and flares are removed after slaughter of the pigs, the findings in these two respects do not directly affect the main question of the influence of the feeding treatments on the cured sides of bacon.

It will also be noted from Table XI that the weights of the fillets tend to increase with increasing protein supply, although the extreme difference between treatments A and C fails to reach actual significance. Feeding treatment appears to have been without effect on the iodine values of both the back fat and the fat of the fillets. This result shows clearly that the level of the protein supply did not significantly affect the character of the fat deposited in the body of the pig, since it was obtained from pigs subsisting on rations designedly poor in oil. There could be no question, therefore, of any obscuring of the true significance of the results as a consequence of a possible influence of food oil on the iodine value of the body fat.

The average iodine values for the individually-fed pigs in the first trial of this series (1936) were 63.2 and 65.8 for back fat and fillet fat respectively. The corresponding values in the present trial were 63.8 and 67.6. There is nothing in these values, therefore, to suggest that the use of a protein supplement of lower oil content had led to any increase in firmness of body fat as measured by the iodine value (see Introduction to present paper).

It may finally be added that tests of palatability revealed no distinctions that might have been attributed to differences of feeding treatment. The flavour of the bacon in every case was very satisfactory.

SUMMARY

The influence of three feeding treatments of differing protein content on growth and carcass quality in bacon pigs has been investigated by the individual-feeding and group-feeding techniques. The protein supplement, which was used in conjunction with barley meal, weatings and a small allowance of lucerne meal, was composed of a mixture of ex-soya-bean meal, dried separated milk and feeding blood meal. Expressing, on the nitrogen basis, the amount of protein food in terms of its equivalent of white fish meal, the standard-protein treatment B supplied the

equivalent of 9 % of fish meal up to 90 lb. live weight, 7.6 % from 90 to 150 lb. live weight and 3.8 % from 150 to 200 lb. live weight. The corresponding figures for the low-protein treatment A were 4.5, 3.8 and 1.9 %, and for the high-protein treatment C, 18, 15.2 and 7.6 %.

Considering the period of feeding up to 200 lb. live weight as a whole, it was found that differences of feeding treatment gave rise to no significant differences in respect of mean rate of live-weight increase and efficiency of food conversion (see Table VI). Only in the earliest stage of the feeding period did the pigs on the low-protein treatment A show a slightly, though significantly, lower rate of live-weight increase and poorer efficiency of food conversion than the pigs on treatments B and C, but such differences had ceased to be manifested by the time the pigs had arrived at 60 lb. live weight, and the slight initial disadvantage experienced by the low-protein pigs was wiped out during the later stages of the feeding period.

The results have confirmed an earlier finding that there is little to be gained in respect of carcass leanness by increasing the level of protein supply beyond that ordinarily used in good feeding practice. Contrary to expectation, however, it was found that a feeding treatment supplying rather less than half the usual amounts of protein-rich food gave rise to carcasses displaying no significant differences in conformation, leanness and general quality from those obtained by the use of rations containing the standard amounts of protein food, this result being achieved without any sacrifice in relation to rate of live-weight increase and efficiency of food conversion.

This result naturally directs attention to the problem of discovering the lower limit of protein supply that is consistent both with the rapid rate of live-weight gain characteristic of the modern bacon pig and the production of carcasses of satisfactory leanness and quality. It is realized that under ordinary conditions of commercial practice it would be incorrect to assume that the optimum supply of protein-rich food is measured simply by the minimum requirements for protein. Other factors must be taken into consideration. It is necessary to bear in mind, however, that certain conditions of economic emergency might conceivably arise in which it would clearly be of advantage to know to what level the supply of protein-rich food in the baconer's ration could be depressed without sacrifice of efficiency.

The present trial has shown that this level is probably much lower than the one commonly accepted, and further experiments have since been carried out which enable this lower limit to be defined with a good

degree of precision. For this reason, therefore, it will be advisable to defer the further discussion of the present findings until they can be considered in relation to the results of these more recent trials. The paper embodying these further results will be published shortly.

ACKNOWLEDGEMENTS

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THE NATURE AND VARIABILITY OF THE CARCASS CHARACTERS OF DANISH AND ENGLISH BACON PIGS

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(With Five Text-figures)

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1. INTRODUCTION, MATERIAL AND METHODS

As a practical background to experimental studies (McMeekan, 1939) and as a basis on which to evaluate some of their quality implications, we have measured the nature and variability of the carcass quality characters of pigs representative of the highest grades supplied to the British Wiltshire bacon trade at the present time. Uniformity in the product is an essential commercial consideration, and it is very desirable that some precise measure be obtained of the extent to which present pigs and methods succeed in this respect so far as the most important branch of the bacon trade is concerned.

Special interest from both practical and scientific points of view attaches to the examination of the extent to which methods of stock selection and improvement and present methods of carcass grading, both based largely upon external characters and upon back-fat measurements of the pig, have resulted in uniformity not only in these characters but also in respect to the "internal" characters which are equally involved in carcass quality but which cannot be examined until the cured bacon is cut up.

The investigation has the additional objective of obtaining in the more precise terms of measurements, a picture of the quality require-

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ments of the trade as represented by carcasses regarded by it as most nearly meeting its demand. The many available accounts of the type of pig required are merely descriptive in respect of the majority of characters, are precise only for weight, length, belly and back-fat thicknesses, for which "standards" have been laid down by the trade itself.

The highly favourable reputation enjoyed by the Danish product suggested that its examination would provide the data required. It was decided to concentrate upon the highest grade, and by arrangement with a large distributing retail organization facilities were provided for the detailed measurements of one hundred Danish No. 1 Selection bacon sides; the data were collected over a period of 3 months. During this time every side passing through the store was weighed, cut and measured. To this extent the data were unselected, but it must be emphasized that selection had already been practised by the Danish exporter through the operation of grading. Carcass grading in Denmark is on a basis of carcass weight and back-fat thicknesses at shoulder, loin and rump. This will result in greater uniformity in respect of these particular characters than probably exists in a random sample of Danish pigs. Accounts of the Danish grading system and of methods of production relevant to the discussion are provided by Jensen *et al.* (1935), Lush (1936) and Bishop (1937).

To provide a basis of comparison and to check up on certain features arising out of this examination, we present data also upon one hundred English sides of the Large White breed of the same weight obtained from a similar examination of the carcasses entered for competition at the National Pig Breeders' Annual Show at Peterborough for the years 1935-7.¹ These sides can reasonably be claimed to represent the highest grade of English product, not only because of their entry for show competition, but because conditions of entry necessitate the attainment of minimum standards of quality comparable to the Danish grading standards. These also may be regarded, therefore, as a selected sample, chosen for "high quality", though within the sides available no selection other than that of weight was practised.

The measurements taken were as used in the experimental studies and as previously described and illustrated (see McMeekan, 1939 and Fig. 1), with certain modifications in consequence of measuring cured sides as compared with complete carcasses.

Thus *carcass length* (here called length loin) was measured from the junction of the first rib and sternum to the centre of the femur head,

¹ The writer is indebted to Dr J. Hammond for these data.

the symphysis pubis having been removed during dressing; this measure is substantially the same as when measured to the latter bone. The lower

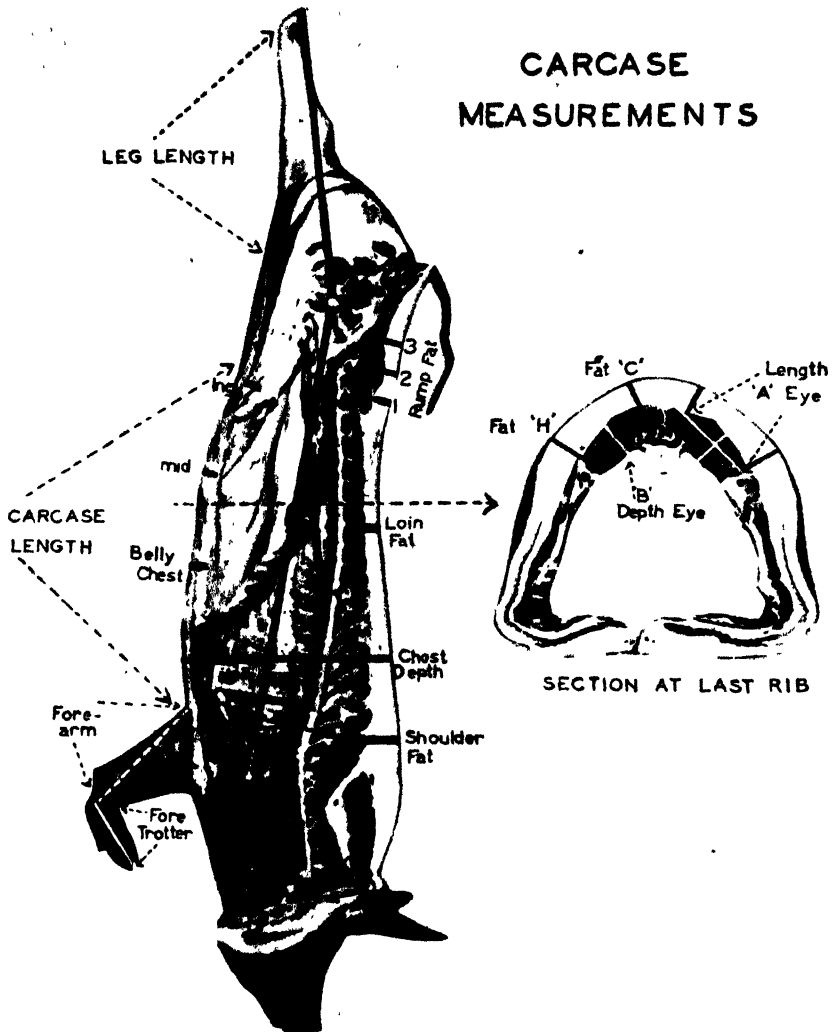


Fig. 1. Carcass measurements.

parts of the legs are absent in cured sides so that leg length was replaced by *length of ham*, measured from the femur head to the lower edge of the meta-carpal bones. Certain additional measurements were recorded as follows:

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Circumference of ham—circumference mid-way and at right angles to the ham length line.

Length short loin—length from the femur head to the head of the last rib.

Side balance—ratio of chest depth to length loin.

Belly 4 (flank)—thickness of belly at its thinnest point as defined by the circular patch of connective tissue in the flank region.

Streak D (lean)—thickness from the internal edge to the outermost layer of muscle tissue, midway along the cross-section at the last rib.

Streak E (fat)—thickness of fat from the outer edge of the last layer of muscle tissue to the skin at the same point as streak D.

Twenty-five measurements in all were taken on the Danish sides, but of these only eighteen are available for the English Large White sides.

2. MEAN MEASUREMENTS: EXTERNAL AND INTERNAL CHARACTERS

The mean measurements, together with their standard errors, are presented in Table I. These are classified on a basis of external characters—linear measurements on the surface of the side designed to afford information on the proportions of the carcass, and internal measures which are of two types: back-fat grading measurements and measures of muscle and fat on the cross-section at the last rib-loin junction.

The figures require little comment. They provide a useful “standard” against which to measure the efficiency of carcasses of other origins, providing it is accepted that they are representative of a high quality status. One or two points, however, might be noted in any such use.

(a) The mean weights of the sides, 54–55 lb., are equivalent to a carcass weight of 140–145 lb.

(b) The length of the eye of loin “A” (Fig. 1) in the Danish sides is extremely good, but the depth of eye “B” is relatively poor; it is significantly less than that of the English sides and 10 mm. less than that of New Zealand carcasses of comparable weight (McMeekan, 1937). It scores but one mark out of twenty-eight on the published scale for bacon quality (Davidson *et al.* 1936). This lack of depth in the loin muscle is probably the greatest weakness in Danish bacon and necessitates “rasher” grading by the retailer on cutting the side.

(c) The belly and streak measurements of the Danish sides are similarly relatively poor by trade statements of requirements, and are significantly less than those of the English sides. Minimum belly thickness plays no part in Danish grading practice, concentration having been on minimum back fat, between which and a thick belly there

exists a certain degree of physiological opposition (Hammond & Murray, 1937), i.e. thickness through the belly is largely due to fat deposition.

Table I. *Variability in carcass measurements*

Character (mm.)	Danish No. 1 Selection			English Large White ex Peterborough N.P.B.A. Show			Signif. of difference in mean measurements
	Mean	S.E.	C.V. %	Mean	S.E.	C.V. %	
External measures:							
Side weight (lb.)	54.6	±0.209	3.83	55.60	±0.273	4.93	N.S.
Length of loin	802.6	±1.950	2.43	813.10	±2.130	2.63	S.S.
Depth of chest	332.3	±1.043	3.14	355.5	±1.310	3.68	S.S.
Circumference of ham	608.6	±1.914	3.15	—	—	—	—
Length of ham	322.1	±1.263	3.93	—	—	—	—
Rib number	15.54	±0.063	4.05	—	—	—	—
Side balance	410.5	±1.871	4.56	444.2	±2.038	4.59	S.S.
Short loin length	389.95	±1.928	4.95	—	—	—	—
Back-fat measures:							
Back fat shoulder	40.69	±0.426	10.48	42.91	±0.503	11.72	S.S.
Back fat loin	22.23	±0.352	15.80	22.42	±0.360	16.07	N.S.
Back fat mean	31.63	±0.329	10.40	32.99	±0.412	12.80	S.S.
Back fat rump	29.49	±0.363	12.30	—	—	—	—
Mean back fat	30.47	±0.303	9.85	—	—	—	—
Internal measures:							
Length of eye "A"	81.20	±0.475	5.85	74.93	±0.598	7.98	S.S.
Mean of belly	27.47	±0.402	14.60	32.91	±0.360	10.94	S.S.
Eye, shape index	407.6	±6.027	14.79	510.9	±9.171	17.95	S.S.
Depth of eye "B"	33.30	±0.494	14.83	37.93	±0.559	14.73	S.S.
Fat at "H"	30.47	±0.484	15.88	28.52	±0.605	21.22	S.
Fat at "C"	22.29	±0.355	15.90	23.19	±0.457	19.71	N.S.
Belly 1, chest	28.64	±0.436	15.04	33.38	±0.434	12.67	S.S.
Belly 2, mid.	28.62	±0.495	17.31	32.55	±0.457	14.04	S.S.
Belly 3, ing.	24.75	±0.552	22.30	32.72	±0.434	13.25	S.S.
Belly 4 (flank)	17.74	±0.411	23.16	—	—	—	—
Streak "D" (lean)	21.66	±0.470	21.70	23.19	±0.430	14.80	S.S.
Streak "E" (fat)	9.55	±0.258	26.96	9.81	±0.270	23.96	N.S.

N.S. = not significant; S.S. = significant at 1 % point; S. = significant at 5 % point.

In respect of the differences between the Danish and English sides it will be noted that in external measures the English are significantly longer, deeper and fatter. In internal characters they also have significantly larger muscle measures, belly thicknesses and fat measures. Undue emphasis must not be given to these differences, which are of interest only in so far as they indicate the extent to which the progeny of the best English *breeding stock* in the Large White breed compare, favourably or unfavourably, with the best *commercial* product of the Danish producer. Special attention might be directed, however, to one major point of difference: the English sides are considerably deeper and in consequence show a large side balance index. Apparently this defect, which is widespread in the English commercial product (Duckham, 1938), is also a characteristic of the best types of the principal bacon breed.

3. VARIABILITY

The variability of each measurement taken has been expressed in terms of the coefficient of variation, and in Table 1 the data are arranged in

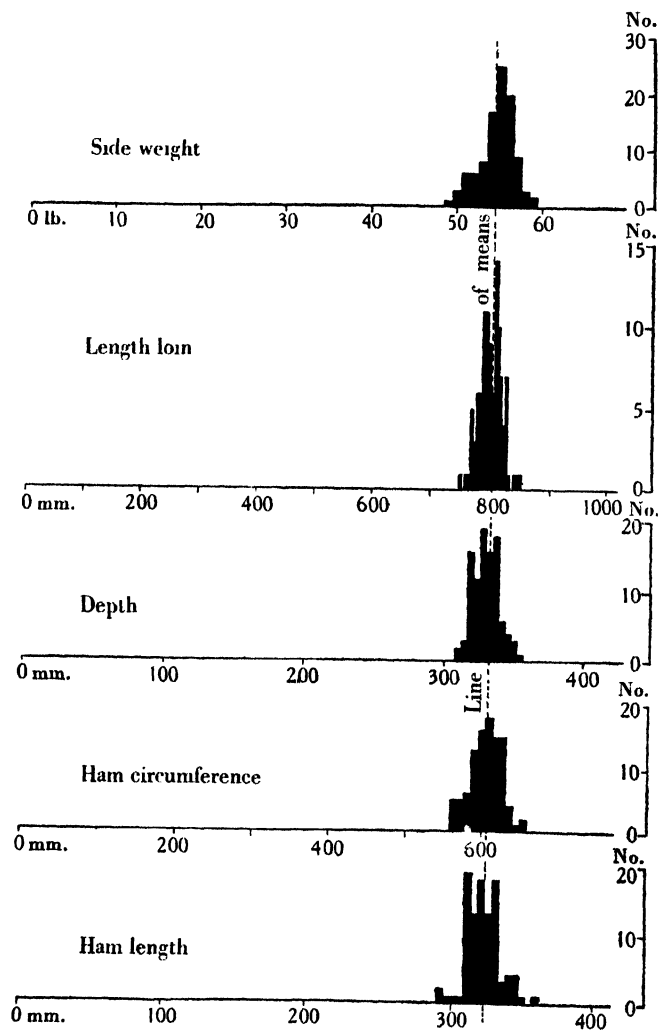


Fig. 2.

approximately in order of increasing variability. The data for the Danish sides have also been expressed graphically in Figs. 2-5. These are

frequency histograms in which adjustment to a common line of means and a variable frequency scale, so that the total area within each histogram is the same, provides a measure of the differences in variability.

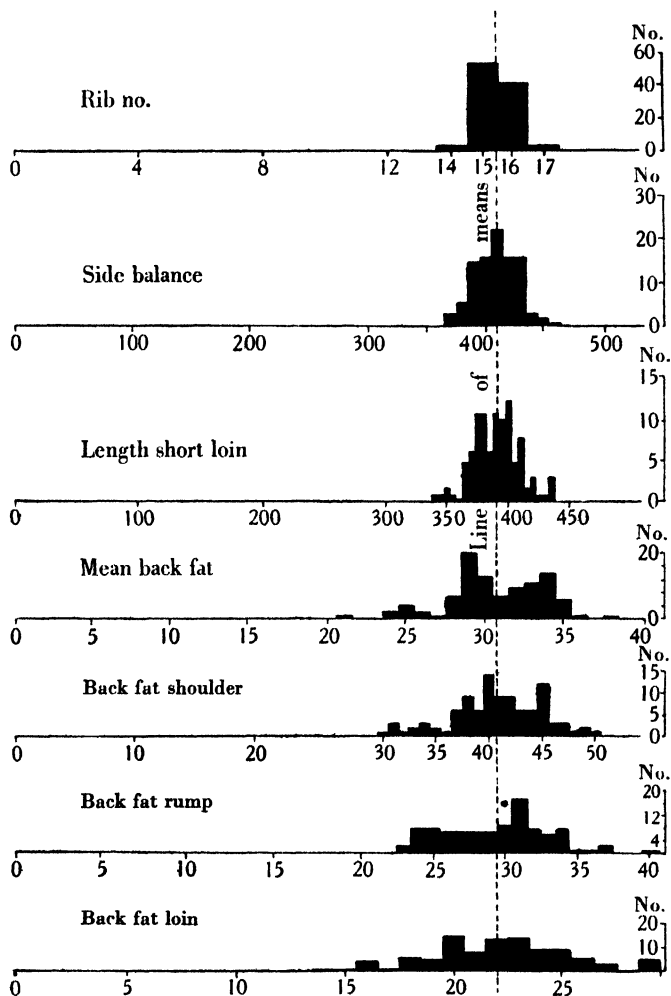


Fig. 3.

The variability in external characters is remarkably low and uniform, with an approximate range of from 2.5 to 5.0% in the coefficient of variation. There is a marked and significantly higher variation in respect to all internal characters with the exception of the length of eye "A".

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The coefficients of variation range from 14.6 to 26.9%. The internal characters used in grading, the back-fat measures, fall into an intermediate position with a variability of approximately 10–15%. For characters for which data are available, the English sides closely confirm the trends apparent in the Danish material.

It is clear that selection on a basis of external quality characters can effect uniformity in respect of these characters, but that this uniformity

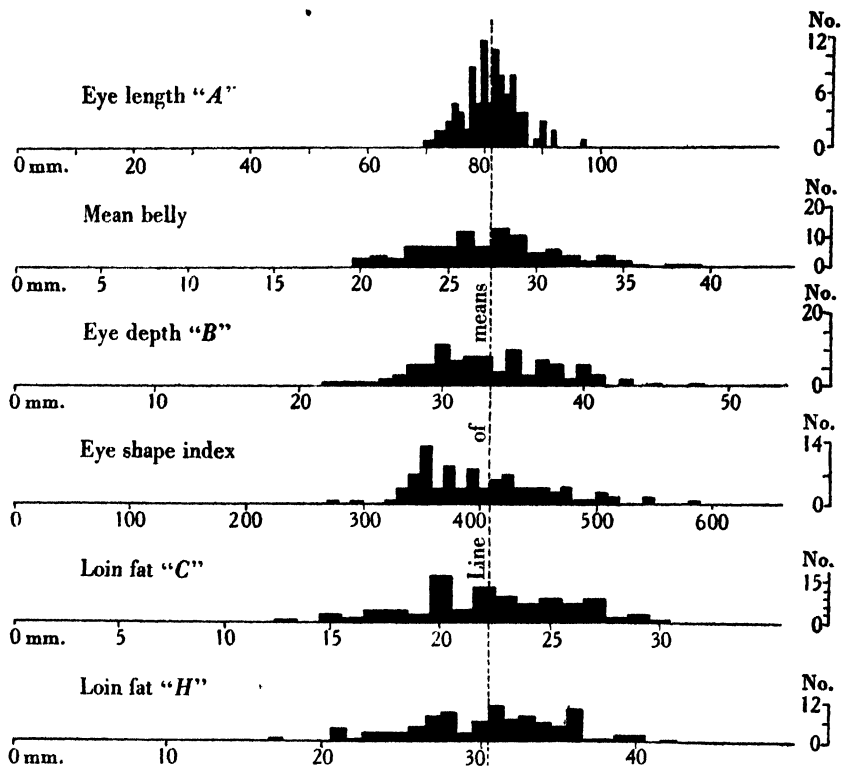


Fig. 4.

is not accompanied by similar uniformity in respect of internal characters for which selection has not been directly practised. For those internal characters which can be measured without cutting the carcass and which are in consequence taken into consideration both in grading and in stock selection practices, greater uniformity can be obtained than for those which present difficulty in measurement. Since the latter govern in a very large measure the cutting value of the carcass, attention might profitably be directed in the production of the ideal bacon side, towards

securing uniformity in respect to these characters also. The data provide a strong case in support of methods of evaluating the internal quality status of the pig in stock improvement schemes in which carcass quality plays a part.

From the theoretical point of view the uniformity in characters, such as length and back fat, and the general conformation of the animal as assessed by other external measures is of considerable interest. In the

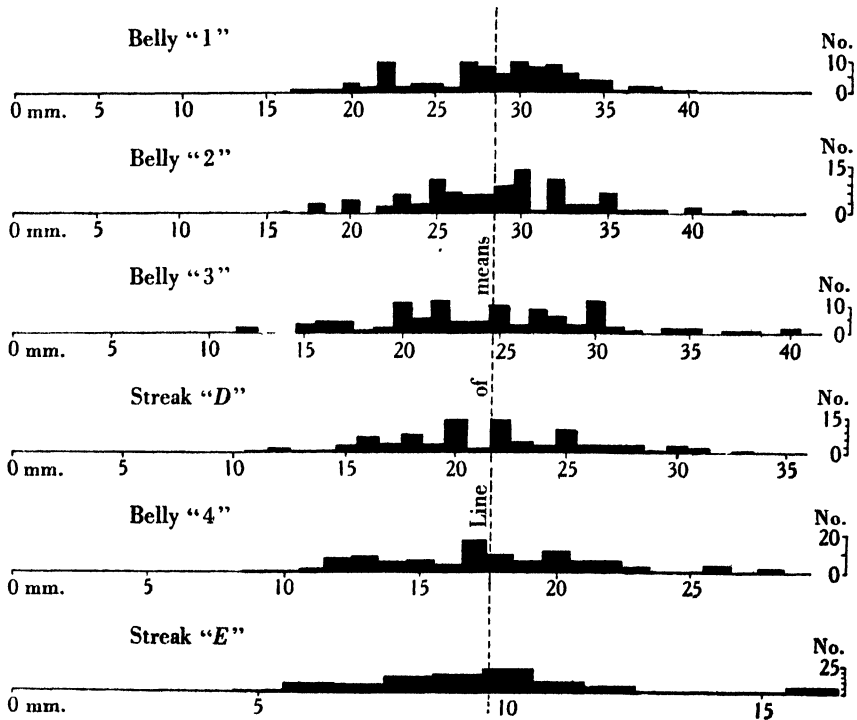


Fig. 5.

evolution of the Danish pig the selection for breeding purposes has long been on a basis of these characters. They have also formed the basis, though to a less precise and intensive degree, of English breeding practice. In a critical examination of the genetic aspects of the Danish system, Lush (1936) concluded that both characters had a genetic basis with about half the variance in length and back-fat due to additive gene effects. It is similarly clear from our demonstration of the effect of nutrition upon these characters (see McMeekan, 1939) that the standard husbandry system employed in Denmark (Bishop, 1937; Jensen *et al.*

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1935) must also have contributed in some degree to the uniformity of the results obtained.

While "selection", both on the breeding and grading side, has been operative in determining the relative degree of variability of the respective characters, it is also evident that at least one other factor has exerted considerable influence. Examination of the variability coefficients show that in general these also vary with the rate of development of the characters concerned. Early developing characters show in general less variation than late developing. This is especially clear in respect of specific comparisons. Thus, in the back-fat measures upon which "selection" has been operative to a similar degree, the variation is greater in the later developing loin and rump measures than the earlier developing shoulder-fat thickness. Similarly, in respect to the muscle measures upon which no direct selection has been practised. Length "A", an early developing character and one unaffected to the same degree by nutrition, shows a much lower coefficient of variation than the depth "B". The relative uniformity of "A" is of interest in view of Hammond's (1936) suggestion that this measure is related to bone length. The data from our experimental studies (McMeekan, 1939) support this. It appears, therefore, that concentration on length of carcass in selection may exert an indirect influence upon a physiologically related part.

The increasing variability of late-developing characters is in line with the general biological principle in this connexion. While it is questionable, therefore, whether some of the differences in variability in carcass quality characters are capable of complete elimination, the modifications possible through control of environment and, on *a priori* grounds, through genetic selection offer practical methods of improvements.

SUMMARY

1. The quality status of Danish and English Wiltshire bacon sides representative of the highest grades produced at the present time has been investigated by the use of carcass measurements. The data resulting provide "standards" for practical guidance in stock improvement work on bacon pigs, and for the evaluation of experimental treatments involving bacon quality.

2. The variability of the respective characters has been compared by means of the coefficient of variation of each. The results indicate that while selection on a basis of "external characters" and of such internal

characters, as are readily measurable, leads to marked uniformity in respect of these characters, it does not necessarily involve similar uniformity in respect of important "internal characters" which are not taken into account in either stock selection or commercial grading practices.

3. External characters thus do not provide a reliable indication of the internal quality status of the bacon pig, and since it is the latter which largely governs the cutting value of the side, concentration upon addition to the former is desirable if still further improvement in the quality of the bacon pig is desired.

4. Variability appears to be affected also by the rate of development of the character concerned; late developing characters in general tend to be more variable than early.

5. The intimate association between nutrition and the rate of development of the various parts and tissues of the pig provides a method of control in addition to that of selection.

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PIG-FEEDING EXPERIMENTS WITH COD-LIVER OIL

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(With Plate I)

INTRODUCTION

COD-LIVER OIL has for many years been recognized as a supplement of very great value when included in small quantities in certain rations fed to a variety of domestic animals. In recent years, owing to the large increase in intensive methods of rearing, it has become of especial importance to the pig and poultry industries.

In commercial pig rearing and, indeed, in much of the experimental feeding of pigs, it frequently happens that the benefit derived from cod-liver oil is not clearly attributed to any particular property, although it is now generally recognized that good quality cod-liver oil is a rich source of vitamins A and D.

For two reasons further experimental work on the feeding of cod-liver oil to pigs seemed necessary. In the first place we have for many years made frequent use of cod-liver oil in our experimental meal mixtures in order to ensure an adequate content of vitamin A and vitamin D without, however, ascertaining the minimal or optimal dose. Secondly, our work on the vitamin requirements of pigs (Foot *et al.* 1938) had made obvious the importance in pig farming of those foods that are rich in vitamin A. Of these, cod-liver oil is obviously one of the most important. We therefore decided to carry out experiments in which cod-liver oil was used in conjunction with a meal mixture containing nothing but foods commonly used in pig feeding practice, but which our previous work had shown to be inadequate in at least one respect, that is, in its content of vitamin A (carotene).

Additional information would also be obtained regarding the vitamin D requirement of pigs on this diet, which question was left open in our earlier work.

When fed in appreciable quantities cod-liver oil is believed by many

workers to be injurious to farm animals. The most recent evidence is discussed, e.g. by Davis & Maynard (1938). It was therefore of importance to us to find out whether practical levels of this substance would exert any untoward effect on the health of the pig and on the quality of the carcass.

The objects of the experiments may be briefly stated as follows:

(a) To find out the most satisfactory and economic level of cod-liver oil which should be included in the meal mixture.

(b) To see if the oil had any deleterious effect when included up to 2% of the diet.

(c) To find the value of cod-liver oil as a source of vitamin A and as a source of vitamin D when supplementing the diet used.

EXPERIMENTAL

The pigs and their management

Twelve litters of pure-bred Large White pigs from healthy stock were used, and the experimental period in each case lasted from about 2 weeks before the pigs were born until they were slaughtered or died. The dam of each litter was confined to the piggery and restricted to one of the experimental diets a fortnight before she was due to farrow. The experimental pigs from each sow were then restricted throughout their life to the same diet as their respective dams.

During pregnancy and before coming to the piggery the dams of the experimental pigs were kept in paddocks in woods. Here they received proprietary pig nuts. They were also able to obtain a little green food, especially during the summer months.

The litters were housed in clean, well-ventilated quarters, and were treated normally apart from restriction to a particular diet. They were given straw or wood shavings as litter and were allowed nothing but their dam's milk during the first 3 weeks of life. The diets were offered as dry meal behind creeps from this time till weaning at 8 weeks old. The young pigs were provided with drinking water *ad lib.* After weaning, the pigs were fed wet, approximately 3 lb. of water being allowed for each pound of meal.

Since the pigs were raised indoors protection against nutritional anaemia was provided. In the litters reared during the winter (lots 1-5) a little Parrish's food was added to the drinking water during the suckling stage. The method was not entirely satisfactory, and it was found necessary as a curative measure to dose certain of the pigs. In the

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litters reared during the summer (lots 6-11) every individual pig was dosed daily during the third week of life with 5 ml. increasing to 10 ml. of Parrish's food daily.

Since the pigs were born in, and confined to carefully cleaned styes it was considered that there would be no great danger of heavy infestation with internal parasites. The summer litters, nevertheless, were dosed after weaning with castor oil and oil of *Chenopodium*. All male pigs were castrated when 5-6 weeks old.

Complete litters were kept intact and placed on the particular diets. Since the pens used would hold only about six or seven baconers it was sometimes necessary to sell animals for small pork in order to make room in their pens.

The rations used

The control ration used consisted of:

Barley meal	50	parts
Weatings	35	„
Extracted soya-bean meal	8	„
Meat meal	5	„
Ground limestone	1½	„
Salt	½	„

An analysis of a single sample of this mixture showed its carotene content to be 0.14 mg./100 g.

The three experimental mixtures consisted of:

Control ration plus ½ % cod-liver oil.

Control ration plus 1 % cod-liver oil.

Control ration plus 2 % cod-liver oil.

The cod-liver oil¹ was of commercial quality and guaranteed purity, standardized to contain 1000 I.U. of vitamin A and 100 I.U. of vitamin D per g. It was mixed into the meal and fresh supplies of the mixture were prepared every few days.

Throughout the fattening period the pigs were rationed according to live weight, but on reaching 6 lb. meal per pig daily no further increase was made.

With certain pigs on the control diet a loss of appetite occurred and they refused to eat the amount demanded by the live-weight standard. They were then fed according to appetite.

¹ Supplied by the British Cod-Liver Oil Producers (Hull), Ltd.

Treatments

Two litters from each of six sows were used. The sows produced the first experimental litters in the period from January to March 1937, and the second litters during the period from June to September 1937. Thus the first were born in the winter months and fattened during spring and summer, while the second were born in the summer and fattened during the autumn and winter. Both litters of each sow received the same ration. Thus it is possible, where necessary, to make a direct comparison between summer and winter litters. On the other hand, when the effects of the various rations are compared, the influence of the individuality of the sow on her progeny is not eliminated, and this has to be taken into account when considering the results.

The pens and sows were allocated to the treatments shown in Table I. Certain of the pigs in the control pens received cod-liver oil as a curative measure in the later stages of fattening.

Table I. *Allocation of treatments*

Pen no	Ear no. of dam	Litter born in
Control ration only		
1	108* and 110*	Winter
2	121	Winter
6	110	Summer
7	108	Summer
9	121	Summer
Control ration + $\frac{1}{2}$ % cod-liver oil		
3	39	Winter
11	39	Summer
Control ration + 1 % cod-liver oil		
4	42	Winter
10	42	Summer
Control ration + 2 % cod-liver oil		
5	40	Winter
8	40	Summer

* Many pigs in these two litters died. Those remaining were put together and reared by sow 108.

Data collected

Careful notes of any symptoms shown by the pigs were made throughout the experimental period. The pigs were recorded under the Berkshire Pig Recording Scheme at 8 weeks old and thereafter were weighed weekly. All pigs sold for bacon were graded by the Pig Marketing Board grader. In addition, the carcasses of the summer-born litters were judged by the curers, and points allocated for certain details regarding quality. At slaughter, blood samples were taken for the estimation of

calcium and inorganic phosphorus, and liver samples taken for the estimation of liver reserves of vitamin A. In most cases the left femur was taken for the estimation of breaking strength, and the second left rib for ash analysis.

RESULTS

Health and symptoms

The rearing records of the litters are set out in Table II. In the six pens receiving cod-liver oil, losses during suckling amounted to sixteen out of sixty born alive, but many of these deaths could be attributed to crushing by the sow which is a usual trouble in indoor rearing, and to weakness of the newly born pigs in one litter. Two losses occurred after weaning, one in each of sow 40's litters. The first was a runt at weaning and eventually died with inflammation of the intestines. The second was also a runt. Its emaciated condition followed a period of scouring during the suckling period. Apart from these casualties the pigs in all six pens receiving cod-liver oil made very good progress, especially during the fattening period. Their appetite was good and they remained robust and healthy in appearance.

In the six litters receiving the control ration only, losses during suckling amounted to nineteen out of sixty born alive. The first litter of sow 110 failed owing to extreme weakness of the pigs at birth, only one pig being saved. The first experimental litter of sow 108 was also very poor. Only seven pigs were born, three were crushed by the sow and two apparently succumbed to nutritional anaemia. The three surviving pigs from these two litters were placed together and reared by sow 108. The third litter (sow 121) born in the winter without cod-liver oil remained intact till weaned. The pigs were, however, subnormal in appearance and growth. On the other hand, the three litters born in the summer without cod-liver oil were above the average in numbers weaned and were not greatly below average size. It is therefore possible that in the early stage of rearing the absence of cod-liver oil was of greater significance in the winter than in the summer.

The difference between the pigs receiving the control ration alone and those receiving cod-liver oil in addition was very obvious in the later stages of fattening, since the former were remarkably consistent in their failure to reach bacon weight. Almost every pig exhibited symptoms of a nutritional deficiency which we had previously found to result from restriction to the same control diet. These symptoms included loss of appetite and digestive disturbance, drooping of an ear with head twisted,

Table II. *Rearing record of litters*

Ration	Pen	Date of birth	Dam	No. of pigs born		No. of pigs weaned	Losses during suckling	Runs died or killed shortly after weaning	Died during fattening period	Ration changed to cod-liver oil after pigs showed symptoms of deficiency	Sold for pork	Sold for bacon
				Alive	Dead							
1937												
Control ration only	1	24 Jan.	108	7	0	2*	3 crushed by sow. 2 died of anaemia	1	—	1	—	—
	1	28 Jan.	110	10	0	1*	Pigs very weak at birth. 8 died shortly after birth. 1 crushed	—	—	—	—	—
	2	19 Feb.	121	7	2	7	—	2	2	—	3	—
	6	24 June	110	12	0	10	1 died first night. 1 weak pig killed	1	1	—	5	3
	7	21 July	108	13	0	12	1 crushed by sow	3	2	3	4	—
1% cod-liver oil	9	15 Aug.	121	11	0	9	1 crushed by sow. 1 killed owing to dermatitis	—	2	6	1	—
	3	28 Mar.	39	7	0	6	1 crushed by sow	—	—	—	—	6
	11	26 Sept.	39	7	2	6	1 crushed by sow	—	—	—	—	6
	4	21 Mar.	42	12	0	8	3 crushed by sow. 1 died—cause unknown	—	—	—	1	7
	10	26 Sept.	42	9	0	6	2 failed to maintain condition and were killed. 1 died of pneumonia	—	—	—	—	6
2% cod-liver oil	5	16 Feb.	40	10	3	8	1 crushed by sow. 1 died of peritonitis	1	—	—	—	6
	8	11 Aug.	40	15	0	10	1 died—insufficient milk. 1 died of enteritis. 1 died of pneumonia. 2 killed owing to weakness—probably shortage of milk	1	—	—	3	6

* Many pigs in these two litters died. Those remaining were put together and reared by sow 108.

impairment of vision and convulsive fits. Death occurred in some cases. In the later stages of the disorder the pigs became lethargic and resented interference. They would sometimes go into convulsions when disturbed. The symptoms corresponded in every way with those which we had previously attributed to a deficiency of vitamin A and which we had found to be cured by vitamin A therapy.

The symptoms of the deficiency in the pigs receiving no cod-liver oil became apparent at ages that varied greatly even within one litter. The ages at which some of the more obvious and typical symptoms were first recorded are set out in Table III. Only pigs that had been on the control ration alone for at least 160 days are included. Prior to this age nine pigs on the diet were cured, died or were slaughtered, but mostly without showing typical symptoms. Every pig of the twenty-five included in Table III showed one or more of the usual symptoms. Twenty-two exhibited abnormal gait, and inability to stand on all four legs was noted in nine cases. Fourteen of the twenty-five showed impaired vision in broad daylight. The pigs were not tested for night blindness.

Many of the pigs originally reared on the control ration alone were later placed on one of the diets containing cod-liver oil or were slaughtered before they experienced the full effects of the deficiency. Nevertheless, of the remainder which received no cod-liver oil, six pigs, nos. 633, 487, 488, 568, 632 and 589, died during the fattening period when 118, 143, 149, 151, 200 and 269 days old respectively. The four earlier deaths occurred unexpectedly and without pronounced symptoms. One pig (597) failed to fatten and was killed as a runt several weeks after weaning.

The pigs were examined post mortem and the following items from the post-mortem reports are of interest.

Pig 487. Died during night when 143 days old. Lungs: adhesions to diaphragm on both sides of thoracic cavity by dry fibrinous attachments. Extensive pneumonic lesions in both main lobes. Anterior accessory lobes on both sides were hepatized. Pericardium: closely attached to myocardium over whole heart. Large intestine: patchy inflammation uniformly distributed throughout. Stomach: acute inflammation at fundic end. Duodenum: marked inflammation of first six feet. Cause of death: pneumonia and heart failure.

Pig 488. Died during night when 149 days old. Lungs: pleura adherent throughout. Adhesions to thoracic wall. Congestions with large areas of hepatization. Pericardium thickened and adhering to

Table III. *Symptoms of deficiency exhibited by pigs receiving only the control diet for at least 160 days*

Pen	Pig no.	Age at which first symptoms appeared	Age (in days) of first appearance of symptom					Age when pig commenced curative treatment	Age when pig sold for pork or bacon
			Vision impaired in daylight	Gait abnormal	Unable to stand on 4 legs	(Convulsive fits	Age when pig died		
2	484	213	—	213	314	288	—	—	322
	489	195	227	216	—	—	—	—	227
	490	174	195	251	—	191	—	—	262
	560	182	252	245	—	182	—	—	257
	562	245	—	245	—	—	—	—	270
6	563	169	—	169	176	—	—	—	197
	565	185	—	185	—	—	—	—	197
	566	201	208	201	201	201	—	—	208
	569	216	216	231	—	270	—	—	270
	589	173	190	190	—	173	269	—	—
7	590	181	181	—	—	—	—	—	181
	591	174	—	174	—	174	—	—	181
	592	188	—	188	188	—	—	190	—
	594	225	225	254	—	260	—	267	—
	596	168	—	168	—	—	—	190	—
9	597	168	—	—	—	—	173	—	—
	598	169	—	—	—	169	—	—	170
	599	162	162	162	—	—	—	—	170
	629	203	203	214	—	—	—	242	—
	630	156	203	156	156	156	—	242	—
	631	214	214	228	—	—	—	242	—
	632	123	—	123	199	199	200	—	—
	634	186	228	186	191	—	—	242	—
	635	190	203	190	190	—	—	242	—
	637	122	—	122	159	—	—	165	—

myocardium. Small intestines: slight inflammation. Cause of death: long-standing pneumonia probably causing heart failure.

Pig 568. It was found to be unwilling to eat in the morning, the ears were slightly purple and breathing became difficult. It died a few hours after it was noticed to be abnormal, when 151 days old. There was some congestion of the lungs and traces of pneumonia. No other abnormalities were found and the final cause of death was not clear.

Pig 633. Died during the night when 118 days old. It had for some days appeared listless, and 2 days prior to death had shown a reeling gait. Lungs: congested. Pericardial sac: contained excess fluid. The intestines were not inflamed and the cause of death was not clear.

Pig 597. This pig remained a runt till it was 173 days old, when it was killed owing to its failure to fatten. A few ascarides were found in the intestines and these may have been partly responsible for its condition.

Pig 632. This pig died in the night when 200 days old. Two days prior to death it had shown slight discoloration of ears and scrotum, and the day before death had exhibited mild nervous spasms. Lungs: right accessory lobe showed pneumonic changes. Intestines: slight peritonitis. Fundic part of stomach inflamed. Probable cause of death: enteritis.

Pig 589. This pig died suddenly when 269 days old. It had previously exhibited symptoms of vitamin A deficiency including impairment of vision, convulsions and abnormal gait. Lungs: left lobe pneumonic. Intestines: haemorrhagic patch at ileo-caecal valve and some generalized enteritis. The cause of death was probably pneumonia.

Growth

Data concerning the growth rate of many of the pigs receiving only the control ration are not available for the later stages of fattening owing to their death or to a change to curative feeding. In order to make use of as much as possible of incomplete fattening periods, the growth rate of every animal which survived for at least part of the fattening period has been calculated for the intervals 50-100, 100-150 and 150-190 lb. live weight. These data, together with the average weaning weights obtained under the Berkshire Pig Recording Scheme, are given in Table IV.

Apart from the four litters receiving $\frac{1}{2}$ and 1% cod-liver oil the weaning weights were subnormal. The records suggest that the differences in this respect are connected with the individuality of the respective sows rather than with factors carried by cod-liver oil, since the weaning

Table IV. *Growth of the experimental pigs*

Ration	Pen	Dam	Born 1937	Pig Recording Scheme data at 8 weeks		Average rate of live weight gain, birth to 50 lb.		Average rate of live weight gain, 50-100 lb.		Average rate of live weight gain, 100-150 lb.		Average rate of live weight gain, 150-190 lb.	
				No. of pigs	Av. wt. of litter (lb.)	No. of pigs	lb. per day	No. of pigs	lb. per day	No. of pigs	lb. per day	No. of pigs	lb. per day
Control ration only	1	108 and 110	Jan.	3	22.8	2	0.43	—	—	—	—	—	—
	2	121	Feb.	7	21.3	7	0.38	3	0.78	2	0.78	1	0.76
	6	110	June	10	26.4	10	0.45	9	0.90	7	0.86	3	0.77
	7	108	July	12	20.6	12	0.38	8	0.79	7	0.81	2	0.52
	9	121	Aug.	9	28.7	9	0.53	9	0.88	8	0.74	5	0.45
		Average of 6 litters			24.1	40	0.43	29	0.85	24	0.79	11	0.58
1% cod- liver oil	3	39	Mar.	6	32.0	6	0.55	6	0.94	6	1.27	6	1.33
	11	39	Sept.	6	30.3	6	0.57	6	0.91	6	1.26	6	1.42
		Average of 2 litters			31.2	12	0.56	12	0.93	12	1.27	12	1.38
1% cod- liver oil	4	42	Mar.	8	31.4	8	0.58	8	1.03	7	1.21	7	1.42
	10	42	Sept.	6	34.1	6	0.60	6	0.93	6	1.25	5	1.41
		Average of 2 litters			32.6	14	0.59	14	0.99	13	1.23	12	1.42
2% cod- liver oil	5	40	Feb.	8	24.5	8	0.48	7	1.11	7	1.26	7	1.40
	8	40	Aug.	10	20.5	10	0.45	9	1.06	9	1.333	6	1.53
		Average of 2 litters			22.3	18	0.46	16	1.08	16	1.30	13	1.46

weights of the litters receiving 2 % cod-liver oil were as low as of those receiving no cod-liver oil.

All six litters receiving cod-liver oil made good growth during fattening. The rate of live-weight gain increased consistently as the pigs grew. In comparing the three levels of cod-liver oil it is clear that the differences in growth rate are well inside the limits of variation that one would expect to find in the progeny of different sows.

The pigs receiving the control ration only showed, during growth from 50 to 100 lb., almost as great a rate of live-weight gain as those receiving the oil. Thereafter the rate of gain decreased, and the few remaining pigs in this group made very subnormal growth from 150 to 190 lb.

Quality of carcasses

Most of the pigs receiving cod-liver oil were sold for class 1 bacon and were graded under the official scheme. Only two pigs receiving the control ration alone reached 7 score (carcass weight), which is the minimum weight for grading. One other pig in this group was used for bacon but was slightly under weight for grading in class 1. The results are set out in Table V. The majority were grade A, but three or four on each level of cod-liver oil were grade L, that is, the lean grade.

Table V. *Grading results of pigs sold for bacon*

	Number of pigs			
	Grade A	Grade L	Other grades	Not graded
Control ration alone*	1	1	0	1
$\frac{1}{2}$ % cod-liver oil	9	3	0	0
1 % cod-liver oil	9	3	0	0
2 % cod-liver oil	9	4	0	0

* Owing to the death of pigs, change to a cod-liver oil ration after showing symptoms, or to sale of animals for pork usually after showing symptoms, few pigs remained to reach bacon weight.

Table VI. *Carcass quality of pigs. Average points
(minimum 0, maximum 10)*

	No. of carcasses examined	Firmness of fat	Colour of fat	Fineness of bone	Fineness of rind	Length of back	Suitability of carcass for bacon
Control ration alone	3	6.7	5.0	8.0	6.0	6.7	5.7
$\frac{1}{2}$ % cod-liver oil	6	9.3	7.7	7.2	6.8	7.0	8.0
1 % cod-liver oil	5	9.2	7.6	8.0	7.2	6.4	8.0
2 % cod-liver oil	4	8.8	7.0	7.8	7.3	6.0	7.3

In order to obtain further information on the quality of the carcasses a number of them from pens 6-11 were closely examined by the curers and points were allocated for quality of fat, bone and rind, for length

of back, and finally for the general suitability of the carcasses for bacon. The results of these examinations are summarized in Table VI. It is clear that the pigs were generally suitable for curing and apparently considered to be of over average quality. The data suggest that the three pigs receiving no cod-liver oil were rather less suitable than those receiving the oil. Those who examined the carcasses found no gross defects in the colour and firmness of the fat nor in the suitability of the carcasses for bacon even where 2% of cod-liver oil was fed up till the time of death.

Liver reserves of vitamin A

Livers from nearly all pigs were obtained as soon as possible after death for the estimation of their reserves of vitamin A. The method has been fully described by Foot *et al.* (1938).

The results for thirty-eight pigs receiving the control ration alone are set out in Table VII, expressed in Moore Blue Units (Moore, 1930).

Table VII. *Liver reserves of vitamin A in thirty-eight pigs receiving the control ration alone¹*

Age at death days	Ear no. of dam	M.B.U. per g. liver	M.B.U. in whole liver	Age at death days	Ear no. of dam	M.B.U. per g. liver	M.B.U. in whole liver
4	108	43	2240	152	110	0	0
6	108	50	2400	152	110	0	0
18	110	63	4610	156	121	0	0
22	108	15	2030	170	108	0	0
22	108	10	1400	170	108	0	0
41	108	15	1180	173	108	0	0
42	108	16	2420	181	108	0	0
53	121	8	1650	181	108	0	0
57	121	0	0	197	110	0	0
63	108	Trace	Trace	197	110	0	0
63	121	Trace	Trace	200	121	0	0
63	108	0	0	208	110	0	0
63	108	0	0	227	121	0	0
95	108	0	0	258	121	0	0
98	110	0	0	262	110	0	0
118	121	0	0	269	108	0	0
143	121	0	0	271	110	0	0
150	121	0	0	271	110	0	0
151	110	0	0	322	121	0	0

¹ Expressed in Moore Blue Units (Moore, 1930).

The data are arranged in order of age of pig at death, and it is clearly shown that the reserves of vitamin A present during the suckling period are gradually used up and no trace was found in any of the twenty-five pigs which died or were killed when over 63 days old. The results for young pigs are in close agreement with those obtained previously (Foot *et al.* 1938), but, as would be expected from the difference in the

treatment of the dams, they are rather lower in the present experiment. In agreement with Foot *et al.* (1938) we find that on the control diet alone the mother's milk does not contain enough vitamin A to increase the liver reserve of the young pig.

Since symptoms of deficiency did not generally appear in these pigs till after they were 150 days old, it is evident that they lived and made subnormal growth for a period of 100 days or more without any liver reserve of vitamin A.

Table VIII. *Liver storage of vitamin A in pigs receiving $\frac{1}{2}$, 1 and 2 % of cod-liver oil (Moore Blue Units)*

$\frac{1}{2}$ % cod-liver oil (dam sow 39)			1 % cod-liver oil (dam sow 42)			2 % cod-liver oil (dam sow 40)		
Age at death, days	M.B.U. per g. liver	M.B.U. in whole liver	Age at death, days	M.B.U. per g. liver	M.B.U. in whole liver	Age at death, days	M.B.U. per g. liver	M.B.U. in whole liver
Born d.	190	3,420	1	85	4,930	28	137	20,960
Born d.	140	4,620	9	420	14,280	45	325	72,800
1	100	3,400	15	62	6,660	47	140	15,680
190	500	595,300	16	140	8,540	47	133	11,730
197	350	396,900	17	77	14,320	63	350	56,350
211	171	215,480	35	165	23,270	76	342	82,760
211	95	118,500	129	195	204,170	160	910	941,670
212	410	653,820	184	488	601,810	160	917	805,550
212	410	674,160	184	200	277,830	209	950	1,235,000
212	500	730,000	197	1276	1,339,590	209	950	1,558,000
218	190	293,560	197	1000	1,105,700	210	975	1,326,780
226	286	396,900	197	1290	992,190	210	1000	907,200
226	171	251,790	211	263	312,560	217	1000	1,233,230
226	117	142,140	211	293	357,050	217	950	1,453,500
296	215	274,290	219	1219	1,788,410	217	1281	1,870,260
			219	1025	1,568,250	223	1429	1,964,330
			219	975	1,491,750	223	1583	2,109,270
			225	182	262,440	223	1328	1,769,490
			225	510	628,940	223	1429	1,700,890
						230	2100	3,206,520
						230	2812	3,467,830
						242	1923	2,344,220

The liver reserves of the pigs receiving cod-liver oil are set out in Table VIII. Most of these data are for pigs which died before weaning or were slaughtered on reaching bacon weight. Hence the reserves for pigs of 10-20 weeks are known in only one or two cases. It is, however, quite clear that at all levels of cod-liver oil the liver reserve of vitamin A was gradually built up as the pigs grew. The reserve at birth was again of the order of 3000 or 4000 M.B.U. This increased only slowly during the suckling period but thereafter at a rapid rate, and at bacon weight even the pigs receiving only $\frac{1}{2}$ % cod-liver oil showed substantial liver stores.

There is a very large variation among the pigs in each group, but

en masse the reserves at bacon weight are roughly in proportion to the level of cod-liver oil fed.

The vitamin D requirements of the pigs on the experimental rations

The cod-liver oil was known to contain vitamin D, and it was therefore of importance to find out if the control ration alone produced rickets under the conditions of the experiment, and if so, to what extent the cod-liver oil prevented the disorder. The pigs were housed throughout in a piggery where they had very little sunlight which had not passed through glass. Judging from its composition the control ration contained no vitamin D. Hence the pigs receiving it apparently received no vitamin D nor had they access to sunlight. The ration, however, contained ample calcium and phosphorus, and the ratio of calcium to phosphorus was considered to be satisfactory. There is some difference of opinion as to the need of pigs for vitamin D when the calcium and phosphorus supplies are adequate. Many investigators consider that under these latter circumstances no vitamin D needs to be added to the ordinary pig-meal mixtures.

We were obviously not able to depend entirely on the clinical symptoms for diagnosis of rickets, since the defective gait produced by vitamin A deficiency might be confused with limb abnormalities of a rachitic condition. Hence it was considered necessary to collect other data that might provide information regarding the problem.

(1) *Calcium and phosphorus content of blood.*

Blood samples from sixty-two pigs were taken at slaughter, and the calcium and inorganic phosphorus of the serum estimated. Most of the samples were taken from pigs at bacon weight, but a few, especially in the group receiving the control ration alone, were from pigs of 100–150 lb. that were killed for pork. The mean values and range in values are

Table IX. *Calcium and inorganic phosphorus content of blood*

	No. of pigs examined	Calcium mg. per 100 ml. blood serum		Inorganic phosphorus mg. per 100 ml. blood serum	
		Range	Mean	Range	Mean
Control ration alone	15	11.86–10.40	11.29	10.8–8.7	9.56
$\frac{1}{2}$ % cod-liver oil	12	13.73– 9.90	11.58	12.3–9.0	10.76
1 % cod-liver oil	12	12.86–10.86	11.71	12.4–9.2	10.53
2 % cod-liver oil	16	12.69–10.41	11.48	11.8–8.0	9.93
Cured pigs*	7	12.60–10.72	11.45	11.3–9.6	10.56

* Pigs which received no cod-liver oil during the first few months of life but which received either 1 or 2 % of cod-liver oil for a period of 26–150 days before death.

given in Table IX. The results suggest that none of the animals was suffering from definite rickets, and the figures for the group receiving no cod-liver oil are of the same order as those of the other groups.

Total calcium was determined by the Clark & Collip (1925) modification of the Kramer & Tisdall (1921) method, and the inorganic phosphorus by the Fiske & Subbarow (1925) method.

(2) *Breaking strength of femora.*

As a further check on the incidence of rickets, the left femora from thirty-three pigs when killed at bacon weight were dissected out and the breaking strength of each measured. The femora were broken across a $5\frac{1}{2}$ in. span and the readings were corrected to breaking strength per square inch section of bone. The results are given in Table X. Only four

Table X. *Breaking strength of femora*

	No. of pigs examined	Breaking strength lb. per sq. in. section of bone	
		Range	Mean
Control ration alone	4	2143-3651	2689
$\frac{1}{2}$ % cod-liver oil	9	2308-3142	2616
1 % cod-liver oil	11	2122-3075	2597
2 % cod-liver oil	9	2273-3499	2765

pigs in the group receiving the control ration alone reached a weight comparable with the pigs in the other groups. However, the mean breaking strength of the femora of these four pigs was similar to the mean values for each of the three cod-liver oil groups, and there is no evidence that the cod-liver oil had any effect on the strength of the femora.

(3) *The ash content of ribs.*

It was possible to carry out analyses of the bones of thirty-eight pigs mostly of bacon weight.

The second left rib including the costal cartilage was used in each case. After careful cleaning, the bones were broken in two and extracted in a Soxhlet tube for 72 hr. with several changes of absolute alcohol. They were then dried at 110° C. for 1 hr. and were ashed in an electric muffle furnace at 700° C. for 5 hr.

The results are given in Table XI. It will be seen that the mean ash percentage was lower for the control pigs than for any of the three groups receiving cod-liver oil. The differences between the control and cod-liver oil groups were found to be statistically significant (the "t" table of "Student" (1908, 1925) was used for the calculations). The odds

against the difference being due to chance were 1 : 167, 1 : 417, and 1 : 38 for the comparisons between the negative control pigs and the group of pigs receiving respectively $\frac{1}{2}$, 1 and 2 % of cod-liver oil.

Table XI. *Ash content of dry defatted ribs (second left) of pigs receiving different rations*

Control ration alone				$\frac{1}{2}$ % cod-liver oil			
Pig. no.	Age at death, days	Fasted live wt. at death, lb.	% ash in rib	Pig. no.	Age at death, days	Fasted live wt. at death, lb.	% ash in rib
489	227	156	47.2	513	190	193	53.4
490	262	179	50.8	512	212	204	52.3
560	258	200	49.7	514	212	221	52.6
562	271	187	47.4	515	212	196	50.9
569	271	193	44.7	517	218	204	51.6
		Mean	47.96	673	197	192	51.5
		S.E.M.*	± 1.06	671	211	200	50.3
				672	226	192	51.1
				675	226	193	52.0
		Cured pigs†				Mean	51.74
468	236	200	50.3			S.E.M.*	± 0.40
467	281	202	53.0				
		Mean	51.65				
1 % cod-liver oil				2 % cod-liver oil			
Pig. no.	Age at death, days	Fasted live wt. at death, lb.	% ash in rib	Pig. no.	Age at death, days	Fasted live wt. at death, lb.	% ash in rib
505	184	188	52.5	469	209	202	49.0
506	184	192	49.8	476	209	209	48.8
507	219	210	52.6	470	217	195	51.9
511	219	210	52.0	474	217	205	48.5
509	219	207	54.1	475	217	205	49.9
510	225	197	52.4	471	230	205	51.3
508	225	210	49.7	473	230	203	53.1
677	197	193	54.6	621	210	194	53.3
678	197	205	52.0	624	223	191	52.3
680	211	195	52.9	620	223	200	49.7
681	211	208	52.5	623	242	209	52.9
		Mean	52.28			Mean	50.97
		S.E.M.*	± 0.47			S.E.M.*	± 0.58

* Standard error of the mean.

† Pig 468 received the control diet alone for 127 days. Pig 467 received the control diet alone for 131 days. Both were then changed to the diet containing 1 % cod-liver oil.

The differences between the three groups of pigs receiving cod-liver oil are very small. It is interesting to note that two pigs which were given cod-liver oil after some 130 days on the control diet had ribs as high in ash as the pigs which received cod-liver oil throughout.

The control pigs showed no clinical symptoms suggestive of rickets, and although their ribs were slightly less calcified than those of the pigs

Table XII. *Curative treatment with cod-liver oil*

No. of pig	Symptoms prior to feeding cod-liver oil	Growth immediately preceding feeding of cod-liver oil lb. per day	Cod-liver oil fed	Growth immediately following commencement of feeding cod-liver oil lb. per day	Effect of feeding cod-liver oil on the symptoms
468	This pig was growing fairly well and had shown no definite symptoms. It was rather thin and leggy	0.58 for 9-week period	1% from 127 to 236 days old	1.30 for 9-week period	Made good progress, showed no symptoms and was sold for bacon
407	This pig developed into a runt after weaning, became rough and dirty in the coat and was very thin and stunted	0.05 for 9-week period	1% from 131 to 281 days old	0.89 for 9-week period	Made a gradual recovery and eventually made good progress. It was sold for bacon
592	This pig had been growing slowly but irregularly for several weeks. Two days before receiving cod-liver oil it exhibited advanced symptoms of vitamin A deficiency. It was unable to stand without aid and the ears were folded back. If supported it walked with a drunken gait	0.39 for 7-week period	20% from 190 to 243 days old	1.31 for 7-week period	Control of limbs improved and able to walk unaided but with a stiff gait 14 days after commencing cod-liver oil. When slaughtered after 53 days on cod-liver oil, it was normal apart from a slightly rough coat
594	This pig's coat had become rough and coarse a month before receiving cod-liver oil. Its gait became unstable and feet tended to knuckle over. It had mild convulsions and immediately before receiving cod-liver oil it needed support for walking. At this time vision had become very defective in broad daylight	0.31 for 6-week period	2% from 267 to 315 days old	1.19 for 6-week period	Improvement in the condition was noticeable in a week. The pig was able to walk without support and the gait improved but thereafter remained awkward. The animal became much less lethargic and vision apparently returned to normal. It was sold for bacon

596	This pig began to develop a stiff gait 3 weeks before receiving cod-liver oil and at the time of changing the diet it walked with small steps with the back arched and hind legs under the body. The coat was long and rough	0-29 for 7-week period	2% from 190 to 243 days old	1-10 for 7-week period	Improvement in general appearance was marked. Appetite improved and the coat returned to normal. The gait improved although the hindlegs persisted in knocking together. The pig was sold for pork
637	This pig had occasionally found difficulty in controlling fore limbs for 6 weeks before receiving cod-liver oil and at the time of changing the diet it could only kneel but not stand on front legs	0-73 for 7-week period	2% from 165 to 218 days old	1-29 for 7-week period	The general condition and the gait improved. The animal regained the use of the front feet but the forelegs occasionally knuckled over till time of slaughter. The pig was sold for pork
629	This pig's vision was first noticed to be impaired 42 days before receiving cod-liver oil. Its gait became very awkward and the pig was nervous and excitable	0-00 for 3-week period	2% from 242 to 268 days old	1-29 for 3-week period	Gait and vision improved. The pig was much less excitable but not quite normal when slaughtered for bacon
631	This pig was stiff in gait and the vision was impaired	0-24 for 3-week period	2% from 242 to 268 days old	1-24 for 3-week period	Vision normal and gait almost normal when slaughtered for bacon
630	This pig had several convulsive fits during 2 months prior to receiving cod-liver oil. Its vision was impaired and the animal was thought to be blind at the time of changing the diet. The gait became awkward and the hindquarters at times out of use	0-12 for 6-week period	2% from 242 to 290 days old	1-07 for 6-week period	The general appearance and vision of the pig returned to normal. The gait improved and the pig was able to walk and even run, but movement remained awkward. The pig was sold for bacon
635	This pig had abnormal gait for several weeks prior to receiving cod-liver oil. At times it appeared to be unable to use hind legs. Vision deteriorated and eventually the pig behaved as if blind	0-50 for 6-week period	2% from 242 to 290 days old	1-21 for 6-week period	Vision returned to normal and control of limbs improved. The gait remained awkward. The pig was sold for bacon
634	This pig behaved as 635. The gait became unstable and vision appeared to be very poor or absent. The pig was also losing weight	-0-17 for 8-week period	2% from 242 to 303 days old	+ 1-05 for 8-week period	Recovery appeared to be almost complete although growth was a little irregular

receiving cod-liver oil it seems clear that the requirement of the pig for vitamin D is of a low order when the calcium-phosphorus balance of the diet is satisfactory.

The behaviour of the pig in this respect seems to be very similar to that of the rat.

A more detailed investigation of the vitamin D requirement of the pig, including histological studies, is certainly needed.

Curative treatment with cod-liver oil of pigs on the control ration

Eleven pigs which had been on the control ration for periods ranging from 127 to 267 days were changed to the diets containing 1 or 2% of cod-liver oil. Prior to receiving the oil, most of the pigs had shown symptoms of vitamin A deficiency and the oil was given in an attempt to cure the symptoms and to promote growth.

In Table XII a brief description of the more obvious abnormalities and symptoms of each pig, prior to receiving cod-liver oil, is set out. Notes regarding the effect of the oil on the general appearance and symptoms are also included.

Although there was a good deal of variation in the condition of the pigs before the curative treatment commenced, each pig showed marked improvement during cod-liver oil feeding. In general, the reaction was similar to that shown by pigs that we had previously reared on the control ration and had cured, either completely or partially, by vitamin A therapy (Foot *et al.* 1938). In cases of general debility there resulted an improvement in growth, and in condition of skin and coat. Where the vision was impaired there appeared to be rapid and complete recovery. Where convulsions had been experienced these ceased. There was normally a marked improvement where the gait had been affected. Where, however, the control of the limbs had become very abnormal it was usual for the gait to remain awkward even when the cod-liver oil feeding was continued over periods of several weeks.

Table XII also gives the rate of growth for each pig for similar periods before and after the change in diet. Although the pigs varied considerably in their rate of live-weight gain prior to receiving the cod-liver oil, they all showed a very marked improvement after the change and most of them commenced to make normal growth. All were eventually sold for pork or bacon. Figs. 1 and 2 show typical photographs of a pig before and after treatment with cod-liver oil.

The reserves of vitamin A in the livers of these pigs at slaughter are set out in Table XIII. The cod-liver oil had not only cured the pigs,

completely or partially, of the symptoms attributed to a deficiency of vitamin A, but had, in all cases, also provided a substantial store of vitamin A in the liver.

Table XIII. *Liver storage of vitamin A in pigs which received the control ration alone during the first part of fattening but which were given cod-liver oil for a period prior to death (Moore Blue Units)*

Pig no.	Age at death days	Age at which cod-liver oil begun days	Period of receiving cod-liver oil days	Ear no. of dam	Level of cod-liver oil in curative diet %	M.B.U. per g. liver	M.B.U. in whole liver
468	236	127	109	110	1	342	528,400
467	281	131	150	108	1	898	1,349,800
592	243	190	53	108	2	525	654,900
594	315	267	48	108	2	1708	2,421,500
596	243	190	53	108	2	854	896,100
637	218	165	53	121	2	833	1,050,900
629	268	242	26	121	2	512	712,000
631	268	242	26	121	2	420	637,000
630	290	242	48	121	2	1050	1,606,500
635	290	242	48	121	2	1167	1,786,100
634	303	242	66	121	2	1500	2,126,300

DISCUSSION

These experiments have shown quite clearly that a factor or factors which are present in cod-liver oil are essential for sustained health and growth in pigs which are otherwise restricted to the meal mixture used throughout the experiments. The fact that this ration was of a type commonly used in pig-feeding in this country makes the experiments of direct practical interest.

There is very strong evidence that the important contribution supplied by the cod-liver oil was vitamin A. The behaviour, symptoms and appearance of the pigs receiving no cod-liver oil were in all respects similar to that of pigs which had previously received the same diet and which had made a remarkable recovery when given concentrates of vitamin A.

The cod-liver oil also supplied vitamin D. The evidence, so far available, suggests very strongly that the meal mixture, which contained a good supply of calcium and phosphorus, produced no clinical rickets, even where the pigs had little direct sunlight. On the other hand, calcification of the bones was slightly increased when cod-liver oil was added to the ration. It must not, of course, be assumed that the same result would be obtained with other rations. Cod-liver oil would obviously

become of increasing importance as a source of vitamin D as the calcium and phosphorus of the ration decreased or as the ratio of the elements was upset.

There is a possibility that the benefit derived from cod-liver oil may have been partly due to properties other than its vitamin content. It may have been useful as a supply of oil *per se* or it may have acted as an intestinal lubricant. But any value in these or other respects was apparently masked by the pronounced effect of the cod-liver oil as a source of vitamin A.

From results of the examinations of liver reserves of vitamin A it seems clear that the cod-liver oil used supplied sufficient of the factor when included in the meal mixture at the rate of $\frac{1}{2}$ %. If, however, cod-liver oil were used in practice mainly as a supply of vitamin A, it might be wiser to use 1 % in the earlier months of fattening and use none in the later stages. We could find no evidence that the cod-liver oil had a detrimental effect on the carcasses but it seems wasteful to sell a pig containing a large reserve of vitamin A in the liver, since these are not at present sold on the basis of their vitamin A content.

SUMMARY

Six litters of pigs farrowed, reared and fattened on a ration of barley meal, weatings, soya-bean meal, meat meal and minerals failed to thrive and in the later stages of fattening many of the pigs showed typical symptoms of vitamin A deficiency.

Six comparable litters raised under similar conditions and on the same meal mixture with $\frac{1}{2}$, 1 or 2 % of a commercial cod-liver oil of guaranteed purity and standardized vitamin content made good progress and nearly all the pigs weaned in these litters were fattened for pork or bacon.

Estimations of liver reserves of vitamin A of the pigs receiving no cod-liver oil indicated that the liver store was exhausted soon after weaning. All pigs receiving cod-liver oil gradually increased their liver store of vitamin A. The stores rose approximately in proportion to the level fed and period of feeding. There was no evidence that the higher levels of cod-liver oil had any practical advantage over $\frac{1}{2}$ %.

The symptoms shown by the pigs receiving no cod-liver oil included loss of appetite, cessation of growth, impairment of vision in daylight, abnormal gait, convulsive fits and nervous collapse. Pneumonia and/or inflammation of the intestines was found in all of seven pigs that died during the fattening period.



Fig. 1. Deficient pig.

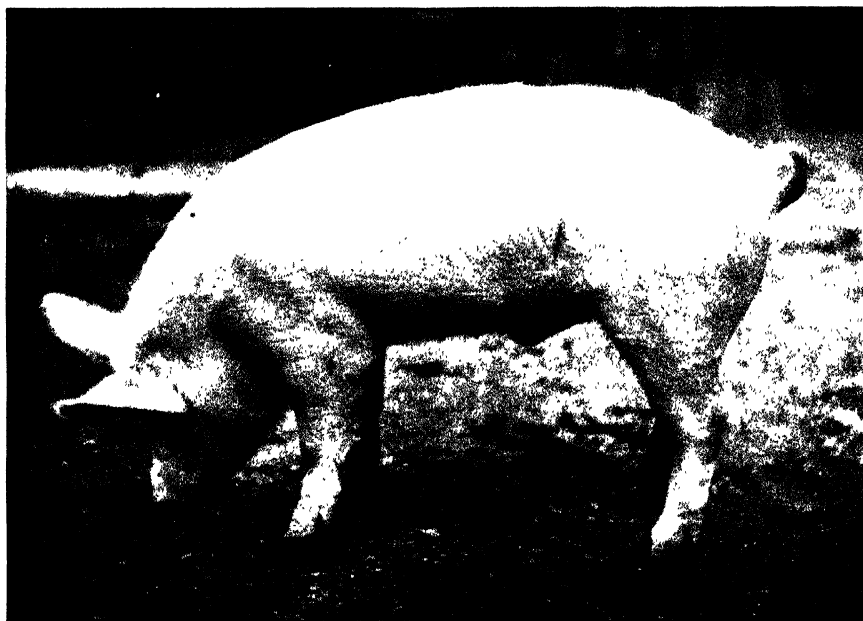


Fig. 2. After receiving cod-liver oil.

Eleven pigs that had developed symptoms on the control meal mixture only, were cured by adding 1 or 2% of cod-liver oil. The pigs returned to normal apart from the persistence of an awkward gait in some cases.

The control pigs showed no clinical symptoms of rickets, and at slaughter the breaking strength of their femora and the calcium and phosphorus in their blood serum were the same as in the pigs which received cod-liver oil. The ash content of their ribs was, however, slightly but significantly lower than that of the cod-liver oil pigs.

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EXPLANATION OF PLATE I

- Fig. 1. Pig 594 when 267 days old and after receiving the control ration alone since it commenced to eat. The pig was unable to move without support, vision had become defective and growth was much below normal. 2 per cent. of cod-liver oil was added to this pig's diet at this stage.
- Fig. 2. Pig 594 when 315 days old and after receiving 2 per cent. of cod-liver oil in addition to the control ration for 48 days. The pig was able to move without support and vision had apparently returned to normal. The gait remained awkward but growth rate had returned to normal.

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FOUR-YEAR LEYS: THE INCLUSION OF RED CLOVER: FIRST YEAR MANAGEMENT

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CONSIDERABLE knowledge of laying down land to pasture has been accumulated in recent years, but a high proportion of the experimental work on the subject has been carried on under the conditions of heavy rainfall obtaining in the north and west of Britain. Farmers on heavy land in the drier districts are constantly being recommended to adopt the alternate husbandry system (i.e. rotations which include long leys and arable crops) which has been established for some time in the wetter areas. It is important, therefore, that the problems connected with the system should be studied in the eastern counties, and during the past seven years investigations have been proceeding on the heavy land of the Cambridge University Farm. In the autumn of 1930 some heavy gault clay, in very poor condition, was taken over by the University Farm and has since been farmed on the long-ley system. Accordingly, opportunity has been presented for studying problems arising in the laying down, and the breaking up, of pasture. The first two problems selected were the desirability of including late-flowering red clover in the seeds mixture, and the relative merits of cutting for hay and of grazing during the first harvest year.

A little experimental work on these problems has already been reported, though the difficulty of measuring productivity of pasture has meant that results have been stated more in general terms than in precise yields. Johnstone-Wallace (1927), Stapledon & Davies (1928) and Davies (1928), as a result of a multiplicity of experiments, came to the conclusion that late-flowering red clover was very aggressive, and liable to crowd out smaller species. Although red clover contributes very largely to a hay crop, its aggressiveness has full play unless the hay crop is cut early. Davies (1929, 1934) concluded that the first harvest year was a critical period in the life of a ley, and strongly urged the desirability of checking aggressive species during that year by grazing, particularly during the spring flush of grass; he found, indeed, that where sowing was carried out on bare ground heavy grazing, even in the seeding year,

was desirable. Against this must be put the fact that in the eastern counties of England the general practice is to take a hay crop from a new ley in its first harvest year. It therefore appears that the two problems selected merit study in the eastern counties, and since they are obviously interrelated the principle has been to study them together. Furthermore, earlier work has been based on observation and rarely has it been planned so that field errors, and hence reliability of result, could be estimated; despite the very real difficulties involved in measuring yields of pasture plots, it was decided to use modern experimental lay-outs and tests of significance.

DESCRIPTION OF EXPERIMENTS

The two experiments described in this paper were exactly similar in lay-out. Each consisted of eight blocks of two main plots each: the main plots had their long sides contiguous, and were utilized for the comparison of a seeds mixture containing late-flowering red clover with one containing none. The two seeds mixtures used were:

	Exp. I lb.	Exp. II lb.
Indigenous perennial rye grass	7	7
Commercial perennial rye grass	7	7
Danish cocksfoot	6	6
Rough stalked meadow grass	2	2
American Timothy	2	2
American meadow fescue	4	4
Suffolk late-flowering red clover	3	0
Canadian alsike	2	2
Wild white clover	1½	1½
	<hr/> 34½	<hr/> 31½

Both the mixtures were sown at the rate of 36½ lb./acre; in the second experiment meadow fescue was omitted. Each main plot was halved transversely for the comparison of haying and grazing in the first harvest year; in that year the sub-plots to be hayed were hurdled off whilst the others were being grazed. After the first harvest year the treatment was constant over all plots. The size of an ultimate sub-plot was 16 × 30 ft., equal to approximately 1/90th of an acre.

The field on which Exp. I took place was very foul when taken over in the autumn of 1930; it was fallowed during the summer of 1931 and was sown down on bare ground on 25 August of that year, after an application of high grade basic slag at the rate of 10 cwt./acre. Plant establishment in the autumn of that year was satisfactory, but in the

following spring the sward was seen to consist largely of slender foxtail; accordingly on 6 June a very light hay crop, consisting almost entirely of the flowering stems of slender foxtail, was taken from the whole area. The comparison of haying and grazing was made on the following growth which was more abundant, grazing being carried out at intervals during July and August, and the other plots cut for hay on 17 August. Exp. II was sown on 7 April 1933, under a crop of Rivett wheat, 10 cwt. of basic slag being applied prior to seeding. After the wheat was harvested very few plants of the ley were to be seen in the stubble, but during August and September a satisfactory establishment appeared. In the following spring, which was an extremely dry one, the plants were small and growth was very slow in starting. Sheep were turned on to the grazed plots during May and June and again just before the hayed plots were cut on 11 July; this cutting for hay was admittedly very late, but was considered rightly timed in view of the slow start of spring growth.

During the spring of each year that the experiments were in operation botanical analyses were made by taking ten random samples, each of 1 sq. ft., from each sub-plot. In Exp. I counts were made for each species of the number of tillers in the case of grasses, and of rooting places in the case of clovers. In Exp. II the same method was used for botanical analysis in the spring of 1934. In 1935, 1936 and 1937, the method was changed to an estimate of the percentage of the herbage contributed by each species, and a separate estimate was made for each sample of the percentage of bare ground. In 1936 and 1937 the shape of the sample was changed from 12×12 in. to 24×6 in., a wooden frame of these internal dimensions divided lengthwise by wires into three equal sections being used, and separate estimates made for each section; this last method has given lower errors, and with care in estimation provides a reliable picture of the pasture. These botanical analyses were directly comparable because they were always taken during late March or early April: in all cases the plots were grazed down in the previous autumn so that there was no appreciable irregularity of growth at the time.

In order that normal grazing might be carried out, the procedure during summer was to allow the experimental area to grow so that the herbage was 6 in. in height, and then to take one sample cut with a lawn mower the whole length of each sub-plot, to provide an estimate of yield; the cuts were taken so that the same piece of ground was not cut over more frequently than once in 2 years. The cuts being taken, cattle and sheep were turned into the area and allowed to graze it down thoroughly; stock were then shut out of the experimental area until

sufficient growth had been made to justify another cut. The number of cuts taken during a year was determined by the rate of growth of the grass. In the case of Exp. II cattle broke into the area in the early May of 1935 so that no experimental cut was possible until 10 June; subsequently the weather was very hot and dry and no further cuts were made during that season. The green material cut from each sub-plot was weighed immediately, and samples taken for the determination of dry matter percentage.

At each cut an effort was made to obtain some idea of the botanical composition of the material weighed; in practice it was only found possible to obtain an estimate of the proportion of the clover in the herbage cut. In 1932 and 1933 (Exp. I) and 1934 (Exp. II) composite samples, made up from each treatment, were divided into clover, grasses and weeds. This gave an accurate measure of the clover content of the samples, but the tedious nature of the work necessitated small samples which represented very poorly the bulk from which they were drawn; furthermore the fact that separate determinations were not made for each plot precluded any statistical analysis, and therefore no appreciation of the significance of the figures could be obtained. In the later years consequently it was decided to dispense with actual analyses, and to rely on eye estimation of the proportion of clover present on each plot; duplicate working and trial checks with actual analyses showed that with practice reliable results could be obtained by this method.

Table 1. *Exp. I. Spring botanical analyses. Ratios between treatments (as percentages)*

		Date of analysis:—			
	Comparison	5. iv. 32	6. iv. 33	7. iv. 34	24. iii. 35
Perennial rye grass	R/N	87	91	122*	113
	G/H	113	129**	115	115
Cocksfoot	R/N	69	78	91	77**
	G/H	116	127*	113	113
Wild white clover	R/N	571***	190**	115	81*
	G/H	80	99	85	85
Weeds	R/N	115	36	72	72
	G/H	105	80	139	70

Note. In this and subsequent tables significances are expressed by asterisks:

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

In Tables I and II the figures given are ratios (multiplied by 100) between means and asterisks denote significances for the corresponding differences.

Table II. *Exp. II. Spring botanical analyses. Ratios between treatments (as percentages)*

		Date of analysis:—			
	Comparison	7. iv. 34	11. iv. 35	17. iv. 36	9. iv. 37
Perennial rye grass	R/N	115	129**	112	103
	G/H	102	110	96	97
Cocksfoot	R/N	90	85**	109	118*
	G/H	99	109	104	89
Wild white clover	R/N	77	66*	69	85*
	G/H	97	62**	84	107
Weeds	R/N	102	50***	70	75
	G/H	106	329***	172*	126*
Bare ground	R/N	—	63**	72*	80*
	G/H	—	172***	151***	114*

RESULTS

Tables I and II give for each experiment the summarized results of the botanical analyses made during March or April of each year, only those species abundantly represented being included; the chief weeds were slender foxtail (in the first year), ox tongue, thistles, red bartsia and bramble. In order to make fair comparisons, figures obtained from these tables were in the first instance adjusted to the form of percentages of the herbage excluding red clover. Bare ground was separately estimated, but the estimates were only made during the last 3 years of Exp. II.

The inclusion of red clover in the mixture apparently favoured perennial rye grass which contributed a larger proportion of the herbage than when red clover was not included. This was true in all cases except the first year of Exp. I. Red clover reduced the proportion of cocksfoot in the herbage in both experiments, although in the second a reversal occurred in the last 2 years. The two experiments are directly contradictory as to the effect of red clover on the survival of wild white clover. In Exp. I wild white clover was very greatly encouraged by the presence of red clover in the early years, whereas in Exp. II it was considerably depressed throughout; this point will be referred to later. Although red clover had little effect on the amount of weeds present in the first year it apparently checked their development during the subsequent years of both experiments; in Exp. II it also markedly reduced the proportion of bare ground.

Grazing, as opposed to cutting for hay, in the first year definitely increased the proportion of perennial rye grass and cocksfoot in Exp. I, but there was no effect in Exp. II. The difference as regards wild white

Table III. *Exp. I. Estimated clover percentages at experimental cuts*

Year	Date	Red clover grazed (RG)	Red clover hayed (RH)	No red clover grazed (NG)	No red clover hayed (NH)	R N %	G/H %	S.E. for R and N means	S.E. of a mean of 8 plots	Significance (Lumped samples)
1932	17. vii. 32 (Hay)	—	79	—	15	541	—	—	—	
1933	6. v. 33	32	28	9	19	219	88	—	—	
	3. vi. 33	35	34	20	21	171	100	—	—	"
	26. vii. 33	29	26	11	20	180	88	—	—	"
1934	4. vi. 34	4	7	10	13	49	70	0.746	0.850	N > R**, H > G**
	13. vii. 34	10	11	14	17	68	84	1.201	1.124	N > R*
	9. x. 34	8	11	7	10	114	75	1.345	1.295	Insig.
1935	13. v. 35	10	13	13	14	84	86	1.140	1.298	Insig.
	10. vi. 35	11	11	14	14	77	101	1.063	1.280	Insig.
	23. vii. 35	17	22	28	27	71	93	1.257	2.570	N > R**

Table IV. *Exp. II. Estimated clover percentages at experimental cuts*

Year	Date	Red clover grazed (RG)	Red clover hayed (RH)	No red clover grazed (NG)	No red clover hayed (NH)	R N %	G/H %	S.E. for R and N means	S.E. of a mean of 8 plots	Significance (Lumped samples)
1934	11. vii. 34 (Hay)	—	52	—	26	200	—	—	—	
1935	10. vi. 35	69	77	29	45	197	81	2.140	2.132	R > N***, H > G***
1936	4. v. 36	16	17	18	17	94	99	1.499	1.243	Insig.
	1. vi. 36	21	23	19	21	111	93	1.473	1.871	Insig.
	24. vii. 36	46	42	54	56	79	102	3.534	3.916	Insig.
	8. x. 36	33	31	48	41	73	118	2.551	2.858	N > R*
1937	7. vi. 37	57	51	58	55	96	108	2.334	2.529	Insig.
	22. vii. 37	69	69	67	68	102	100	2.809	2.363	Insig.

clover was slight, except for one year of Exp. II, but the general tendency was for grazing to give rather less of this species in the herbage. The incidence of weeds on both experiments was very erratic and no constant differences were discernible on Exp. I; on Exp. II, however, grazing produced an extremely large increase in weeds, and this no doubt was related to the other fact, shown in Table II, that grazing produced a large increase in the proportion of bare ground.

Tables III and IV show the results of estimations of clover made, as described earlier, at the times when experimental cuts were taken. The very large increases shown for red clover plots over the others in the first 2 years were, of course, due to the red clover itself. Subsequently the red clover plots gave the lower figures; though the ratios were somewhat erratic, the decrease in the persisting clover, i.e. mainly wild white, in the third and fourth years was of the order of 20 %. The differences between the plots grazed and the plots hayed in the first year was small throughout the duration of both experiments. In Exp. I the grazed plots gave a figure fairly consistently (about 15 %) higher than the hayed plots, whereas in Exp. II the tendency was in the opposite direction.

The yields of dry matter obtained are given in Tables V and VI. The measurement of yield of nutrients from experimental plots on pasture always presents the gravest difficulties, since the variability among animals, and the necessity of having large plots, renders measurement by live weight gains unsatisfactory. Limitations of dry matter yields are obvious, but it is felt that, taken in conjunction with botanical analyses, they do provide at least some approximation to yields of nutrients.

As regards yields of hay in the first year the presence of red clover in the mixture provided very large increases; the yield was nearly three times as much in Exp. I, and nearly twice as much in Exp. II, on the red clover plots as on the controls. The red clover persisted well into the second year, in which its plots produced highly significant increases in yield over their controls; in subsequent years there was little difference, and it can be concluded that the red clover was very valuable in the first 2 years without having any harmful effect in the last 2 years.

The relative effects of grazing and cutting for hay in the first year on subsequent growth were diametrically opposed in the two experiments. In Exp. I the grazed plots considerably out-yielded the hayed ones, the difference being highly significant in the second year and with the total for the 3 years. The difference in total yield in the 3 years was 13 %,

Table V. *Exp. I. Yields of dry matter (cut./acre)*

Year	Date	Red clover grazed (RG)	No red clover grazed (NG)	No red clover hayed (NH)	R N %	G H %	S.E. for R and N means	S.E. of a mean of 8 plots	Significance
1932	17. viii. 32 (Hay)	—	—	2.45	281	—	0.559	—	R > N***
1933	6. v. 33	9.31	6.89	5.29	126	143	0.215	0.418	R > N**, G > H***
	3. vi. 33	14.39	11.87	10.56	117	117	0.461	0.393	R > N*, G > H***
	26. vii. 33	14.21	13.24	11.01	115	112	0.428	0.871	R > N*
	Year's total	37.91	32.02	26.86	118	120	0.780	1.028	R > N**, G > H***
1934	3. v. 34	10.60	9.60	9.29	104	110	0.396	0.483	Insig.
	4. vi. 34	7.40	7.82	7.55	96	102	0.210	0.448	Insig.
	13. vii. 34	7.64	8.10	7.55	94	108	0.252	0.471	Insig.
	9. x. 34	5.09	5.00	4.94	98	105	0.142	0.205	Insig.
	Year's total	30.73	30.52	29.33	98	107	0.739	1.083	Insig.
1935	13. v. 35	11.57	10.08	8.89	109	120	0.245	0.770	R > N*, G > H*
	10. vi. 35	8.11	6.64	6.53	113	111	0.131	0.666	R > N**
	23. vii. 35	10.85	13.96	11.54	89	106	0.940	0.663	Interaction*
	Year's total	30.53	30.68	26.96	101	112	1.084	0.894	G > H**
Grand total—3 years		99.17	93.22	83.15	106	113	1.853	2.352	G > H***

Table VI. *Exp. II. Yields of dry matter (cut./acre)*

Year	Date	Red clover grazed (RG)	No red clover grazed (NG)	No red clover hayed (NH)	R N %	G H %	S.E. for R and N means	S.E. of a mean of 8 plots	Significance
1934	11. vii. 34 (Hay)	—	—	12.42	177	—	0.706	—	R > N***
1935	10. vi. 35	15.34	9.90	12.83	150	80	0.511	0.683	R > N***, H > G***
1936	4. v. 36	5.87	5.24	6.35	117	79	0.382	0.298	H > G***
	1. vi. 36	7.80	5.32	6.57	128	93	0.805	0.709	Insig.
	24. vii. 36	15.36	14.33	15.39	112	90	0.676	0.591	H > G*
	8. x. 36	8.67	8.95	8.24	106	97	0.523	0.744	Insig.
	Year's total	37.90	33.13	36.75	114	90	1.986	1.388	H > G*
1937	7. vi. 37	10.78	10.79	10.61	110	93	0.325	0.554	Insig.
	22. vii. 37	10.54	10.60	11.45	99	93	0.345	0.561	Insig.
	Year's total	21.32	21.39	22.06	104	93	0.499	0.879	Insig.
Grand total—3 years		74.56	64.42	71.64	117	89	2.773	1.570	R > N*, H > G***

which was equivalent to 11 cwt./acre of dry matter. In Exp. II the hayed plots considerably out-yielded the grazed ones, the difference being again highly significant in the second and third years, and also in the total for the 3 years; the difference in total yield in the 3 years in favour of haying was 11 %, which was equivalent to 9 cwt. of dry matter per acre.

From these two experiments it can be concluded that late flowering red clover is well worthy of inclusion in the seeds mixture for a 4-year ley; it increases the yield during the first 2 years markedly, without causing any subsequent reduction in yield. The cover it provides reduces weed infestation and, although it does tend to reduce the amount of wild white clover present in the herbage in the third and fourth years, the reduction is not serious. Conclusions on the relative merits of grazing and cutting for hay in the first harvest year are not so clear-cut, because of the diametrically opposite results given by the two experiments. It is believed that the disagreement is explained by the state of growth of the seeds ley and the weather during the season in which the comparative treatments were given. In Exp. I the ley was well established when the comparison was made because that was later in the summer than would normally be the case; in these circumstances grazing was very definitely the better treatment. In Exp. II the seeds ley was very slow in establishing itself, and the ground was not well covered in the early spring of the first harvest year, though by the end of that year the field could be described as an excellent pasture; probably the main factor in that case was the superlatively dry weather which characterized the winter, spring and summer months of 1934. In those circumstances it was apparently very desirable that the young plants should be allowed to grow up somewhat, in order that their root systems might become thoroughly established, and consequently cutting for hay produced very much better pasture than grazing in that abnormally dry spring. The experiment occupied a small part of a 17-acre field, the main part of which was folded with sheep during May and June of the first harvest year; observations made on the bulk of the field subsequently entirely supported the conclusions drawn from this experiment. The part of the field which was folded early was severely checked, and it was possible to see, at least throughout the second year, a progressive improvement from the first to the last folded part.

SUMMARY

1. Two experiments have been carried out on the Cambridge University Farm to test the desirability of including late-flowering red clover in the seeds mixture in the case of a 4-year ley, and to compare grazing with cutting for hay in the first harvest year.

2. The majority of the red clover survived for the first 2 years, during which it increased the yield of dry matter very markedly; it did not lead to any reduction of yield in the last 2 years. By producing an early cover of the ground red clover checked the encroachment of weeds; although it reduced the proportion of wild white clover in the herbage in the later years, the reduction was not serious.

3. Where the young plants were well established at the time, and normal weather conditions were experienced, grazing was definitely preferable to cutting for hay during the first harvest year. Where the plants were slow in establishing themselves, and in a superlatively dry spring and summer, grazing checked the development of the sward too much, and cutting for hay gave much better results.

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A STUDY ON THE DATE OF EAR EMERGENCE IN BARLEY

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(With Nineteen Text-figures)

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1. INTRODUCTION

THIS paper is concerned primarily with indicating the desirability of associating a closer study of the nature of physiological characters with their genetic behaviour in any attempt to analyse the hereditary behaviour of hybrid progenies. The physiological character here taken as an example is that of the date of ear emergence in barley, and although a final elucidation of the problems involved has not been reached, the association of these lines of approach appears to throw more light on the peculiarities of the genetic phenomena.

Some biologists have expressed the opinion that chromosomal inheritance is quite inadequate to explain the inheritance of the more complex manifestations of life as expressed in physiological characters. This is partly due to ignorance concerning the nature of many physiological processes in the living organism, and it seems that successful

hereditary analysis can only be achieved when a greater understanding of the processes has been first attained. In many cases it is not at all certain whether some physiological characters can legitimately be regarded as "characters" in the genetic sense, but they are more in the nature of physiological complexes which require resolution into their components before genetic analysis is attempted. Again, many of these characters are so strongly affected by, and intricately bound up with the environment, that careful investigation is necessary before the true nature of the character is appreciated. Therefore, the evidence presented in this paper is discussed more in relation to the analysis of the character, and the character-environment complex, rather than the establishment or confirmation of genetic laws and principles. This does not mean, however, that the genetic analysis of the data is entirely neglected, but rather that an attempt has been made to interpret the peculiarities of the hereditary phenomena in terms of the nature of the character and the influence of the environment. Also, some stress is laid on the fact that although perhaps a superficial genetic analysis indicates a simple factorial explanation, such analysis leaves much to be desired in giving a true picture of the actual facts.

Modern genetics has been forced to modify considerably the older and somewhat mechanical conceptions of factors and characters, while the relationship between the factor and the character has lost its simple and artificial conception and acquired a broader biological aspect. It is now realized that the independent unit factor as a biological unit is an untenable hypothesis, and that the action of any single factor must be considered in relation to the products of all the other factors in the organism, thereby giving rise to the manifestation recognized as a plant or animal character. Similarly, one factor must affect many characters, probably in manifold ways, but for the convenience of genetic analysis a factor is identified or associated with some one, easily identifiable, character. Such being the case, it is only to be expected that a position can be reached where it may be impossible to identify a convenient character with a particular factor, or factors, particularly where the environment exerts a potent and dynamic influence.

The evidence discussed in this paper results from a study of ear emergence in barley only, but since the phenomena involved are similar to those observed in other cereals, a brief reference will be made to work relating to the earliness character in cereals generally in order to emphasize certain important points.

The inheritance of earliness has been studied by using the characters

“earliness of ripening”, “time of flowering” and “time of ear emergence” as the criteria. Ripening is usually correlated with ear emergence in so far as forms with early ear emergence are characterized in general by early ripening, but the period from ear emergence to ripening varies with particular varieties. Time of flowering usually denotes time of ear emergence, and the latter is a more convenient and more sharply defined character with which to work. Consequently, in the brief survey given below, various aspects of earliness in cereals are referred to in so far as they bear on the immediate discussion.

In wheat, time of ear emergence has been interpreted as due to a single-factor difference by Biffen (1905), a three or more factor difference by Freeman (1918), a four-factor difference by Aamodt (1927) and a multi-factorial difference by Gfeller (1937) and others. Crescini (1930), in a study of ear emergence in four separate crosses with *vulgare* wheats, observed the following four conditions: (1) almost complete 3 : 1 dominance of the later parent; (2) a bimodal segregation with incomplete dominance of the later parent; (3) a bimodal segregation intermediate between the two parents; (4) intermediate earing with a marked shift towards the later parent. Koboltova (1930), using different *durum* varieties crossed on to the same *vulgare* variety, observed a considerable difference in the earing time of the F_1 's and in the proportion of non-earing plants in the F_2 's, depending on the various *durum* parents used. This occurred in spite of the fact that the *durum* forms themselves differed only in 1–2 days in their own ear emergence times. Newman (1933) states that although the early ripening character is heritable, it is not a simple Mendelian character. Dominance of earliness, dominance of lateness, and absence of dominance have been observed in different crosses, while some workers report transgressive segregation, and others a failure to recover the parental types.

Noll's hybrids between early and late varieties of oats showed in some cases the F_1 earing with the early parents, and in other cases earing earlier than the early parent, while hybridization of parents earing at the same time gave an F_1 distinctly earlier than the parents. Noll (1925) concluded from the F_2 and F_3 generations that earliness was dominant and dependent on multiple cumulative factors, and he was able to obtain homozygous lines earlier, as early, intermediate and later than the late parents. Other workers have reported the dominance of earliness, with the F_1 earing with the early parent, and the F_2 showing a bifactorial difference. Nilsson-Ehle (1908), working with time of maturity, observed transgressive segregation with homozygous lines earlier and later than

either parent, while Caporn (1918) in a cross in which the F_1 was intermediate failed to recover forms as late as the late parent.

Experiments conducted with barley by Kuckuck (1933*b*) showed that the length of day, spring temperatures and moisture affected the time of earing of parental types. Hybridization between two early spring types, one of which would ear in short days and the other would not, showed pronounced transgression in the earing of the F_2 , and all the F_3 types with erect habits which flowered before a particular time bred true, the later ones segregating for type of habit. The results were too complicated to be explained on a three-factor difference. Kuckuck found in other crosses that after spring sowing the spring type was dominant, and after winter sowing the winter type was dominant. He concluded that lateness, winter hardiness and winter habit were so closely correlated as to be unrecognizable as distinct phenomena. Huber (1932), on the other hand, assumed a four-factor difference for earing time in a cross between a winter and a spring variety, the former being recessive for all four factors. Wexelsen (1934), in a study of some linkage relationships in barley, observed a correlation between earliness and certain morphological characters of the ear, and he considered that a factor for earliness was present in each of the two established linkage groups.

Similar results with regard to differences in genetic analysis are to be found in hybridizations with rice. Ramiah (1933) quotes a simple 3 : 1 ratio, and a transgressive segregation for which he postulates several early factors, one late factor and an inhibitor. Ganguli (1937), in a study of summer, autumn and winter varieties of rice, also reports complicated relationships in which transgressive segregation was an obvious feature, although in some cases this was accompanied by a definite bimodal F_2 distribution of 3 lates : 1 early. Crosses even between the same types of varieties resulted in different hereditary behaviour in Ganguli's investigations.

It may be seen, from the few citations given above of investigations involving the inheritance of ear emergence or earliness, that many genetic interpretations have been advanced to explain the results obtained. This does not only apply to different species, but it also holds within any one species, where different varietal combinations are characterized by particular hereditary behaviour. The fact that simple Mendelian segregation has been observed in some cases, and that extreme complexity with no feasible genetic interpretation has been experienced in other cases, suggests, of course, that no general genetic hypothesis can be advanced which will explain the hereditary phenomena even within one

species. Indeed, it has been suggested that every cross will require separate study, and any preconceived hypothesis even with regard to dominance is entirely unwarranted. Owing to the great importance of the earliness character in practical plant breeding, such a position is of great significance, because it implies that hybridization experiments involving the use of earliness cannot be intelligently planned beforehand. This, unfortunately, applies to many of the characters with which the breeder works, and involves the making of crosses in an entirely experimental manner to test the possibilities of various parental combinations. In many cases the entirely unforeseen occurrence of transgressive segregation may result—a factor of great importance in breeding work—but the purely empirical nature of such investigations is not desirable.

2. EARLY TIME AND EARLINESS AS A "PLANT CHARACTER"

The time at which a particular cereal variety comes into ear or matures is the manifestation of a complex series of physiological processes within the plant. These processes are very much affected by the conditions of growth, both in relation to the wide differences of climate, and also the smaller fluctuations of weather conditions from season to season within local areas. Cereal varieties from different geographical areas may be characterized by particular climatic requirements for the manifestation of their early maturing characteristics. Pal'mova & Basova (1934) state, for example, that early maturing wheats are found in four geographical regions, viz. the Arctic, continental regions of the subtropics, mountainous regions, and countries of periodic rains such as China. These four groups may be classified as southern forms, which are tolerant of high temperatures and possess a low light requirement, and northern forms, which possess a low temperature and high light requirement. The inheritance of earliness differs in these two physiological types, the earliness of the southern early forms being dominant and transmitted to practically all the progeny, while that of the northern forms, such as the Steppe wheats, is sometimes dominant and sometimes recessive. The authors state that this difference is due to the light requirement, and by crossing forms of extreme requirements, it is possible to produce types of varying earliness due to their varying light demands.

The importance of light and temperature in the phasic development of cereals requires no elaboration here, but it is of the utmost significance to any genetic study of earliness. It is possible to differentiate between winter and spring varieties of oats, rye and wheat by studying the

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development of the growing points of young plants when grown under continuous illumination (K.-Maximov *et al.* 1933). Similarly, the response to low temperature treatment is an unfailing test of the winter and spring habits of cereals. The various vernalization experiments on cereals, which have been so widely conducted in recent years, have done much to elucidate the physiology of development, particularly in relation to the time of earing, and it may be concluded that temperature and photo-periodic exposure are the two chief environmental factors conditioning ear emergence. Indeed, light and temperature are of such importance that they are not merely instrumental in conditioning the degree of expression of earliness, but they may entirely inhibit its expression altogether. But the interrelation of light, temperature and the earing of cereals is further complicated by the environmental stimuli acting differentially during the development of the plant—early exposures to certain conditions affecting the subsequent development of the plant.

Although the conception of plant development put forward by the Lysenko school cannot be regarded as fully explaining the facts, the great value of the Russian work has been in directing attention to what is now known as phasic development in plants. The developmental phases or stages through which cereal plants pass from germination to maturity are particularly well marked, and have consequently been the subject of much study in relation to the effect of environmental stimuli on the passage from one phase to the next. Lysenko's work has been concentrated principally on the passage from the vegetative to the reproductive phase, and he studied the stimuli necessary to bring about that passage. The most significant fact which has emerged from the extensive work on this subject is that the plant may be exposed to conditions necessary for reproductive stimulation at a very early stage in its development. This means, of course, that the stimulation to earing in cereals is not a simple function of the conditions at and around the period of ear emergence, but that the whole of the conditions from germination onwards are vitally concerned not only with the time of ear emergence, but also with the ability of the plant to come into ear at all. More recent work has even shown that the conditions of ripening of the grain can affect the subsequent development of the plants in the field.

The physiological resolution of plant development in cereals, which has so far been attempted, has shown the considerable variability between different varieties or types in relation to environmental stimuli and phasic development. Different varieties may require different combinations of daylight or temperature exposure to bring about their most

rapid development. Thus, in discussing "earliness" or "lateness" it is necessary to understand something of the physiological characters which determine this earliness or lateness, because it is possible that two varieties may owe their simultaneous earing under a given set of conditions to different physiological constitutions, but the environment has failed to differentiate between them. Grown under other conditions the two apparently similar varieties might be quite distinct in their behaviours and in their time of ear emergence. It has been stated, for example, that the chief factors in the conversion of winter varieties into spring varieties are temperature and light exposure. These two factors are complementary in their action, sometimes the one and sometimes the other being the decisive factor according to the conditions. The old conception of "long-day" as opposed to "short-day" plants must also be modified, because such a differentiation merely emphasizes the characteristics of one particular phase of the plant while completely ignoring the requirements and characteristics of other phases.

It thus follows from the above statements that the study of the time of ear emergence or earliness as a plant character must be made in relation to the physiological basis of this character expression. Ear emergence is merely an arbitrary, easily visible, stage in the development of the plant, which has resulted from a series of phasic changes absolutely dependent on the environment for their successful accomplishment. The most important of these changes is the passage from the vegetative phase to the reproductive phase, a transition which requires the correct environmental stimulation for its own initiation, and which is affected in the subsequent changes which it initiates by further environmental conditions. Therefore, in so far as individual varieties require particular environmental stimuli for the absolute expression and the speed with which this expression is manifested, it follows that the behaviour of the same variety under different conditions, and of different varieties under the same conditions, will vary. If such is the case, hybrid progeny resulting from the cross of any two varieties will similarly vary in their behaviour according to the physiological characteristics of the parents, and the same parental combinations under different growing conditions, or different parental combinations under the same growing conditions, may result in distinct hereditary phenomena as exemplified by the characteristics of the F_1 , F_2 and F_3 generations.

3. THE DATE OF EAR EMERGENCE AS A VARIETAL CHARACTER

The investigations described subsequently in this paper are concerned primarily with the inheritance of the date of ear emergence, or, in other words, of the number of days from sowing to the emergence of the ear. Before describing the results obtained, it is most important to realize the status and nature of this character as a varietal character when the material is observed in one locality. If the criterion of ear emergence in barley is taken as the exertion of the awns of the main tiller through the last leaf sheath of the stem axis, it will be found that within the normal range of sowing time in the spring the majority of varieties will come into ear in more or less the same sequence year after year. In a pure line, normally developed plants will occupy a period of 4-5 days to accomplish ear emergence in a plot of 200-250 plants. There are always plants which lag behind this period of ear emergence by reason of some check to their growth, but, after some experience in observation, such weakly plants can always be observed satisfactorily. It is, of course, important that observations be made each day at approximately the same time, and the most satisfactory criterion of the date of ear emergence of a pure-line population is the date at which approximately 50 % of the plants have come into ear.

The climatic conditions during growth will affect the number of days from sowing to ear emergence, so that even if sowing is effected on the same date in different years the time taken for a variety to come into ear will almost certainly vary. On the other hand, the relative times of ear emergence of different varieties remain reasonably constant under

Table I. *Variation in the number of days from sowing to ear emergence with differences in sowing time in different years*

Variety	February				March				April
	1934	1934	1932	1930	1936	1933	1935	1931	1937
Pryor's Chevallier	14	19	17	26	7	15	21	26	1
Big Wheat Barley	—	91	101	89	73	69	69	68	59
Plumage	101	—	107	97	83	76	73	73	66
Plumage-Archer	—	113	124	109	101	87	90	88	84
Goldthorpe	—	114	125	111	101	89	91	89	83
Bocumer	—	114	127	111	103	93	94	90	86
<i>H. spontaneum</i>	116	—	128	110	105	106	102	101	98
<i>H. vulgare parallelum</i>	103	—	110	99	93	87	92	89	90
<i>H. vulgare praecox</i>	110	—	119	102	92	82	85	82	74
<i>H. inter. transiens</i>	110	—	117	*	96	88	96	*	71
B. 24	114	—	119	105	97	86	89	84	78
	121	—	*	*	108	105	102	*	100

* No data available.

such conditions, and the sequence of earing is such that it is possible to characterize varieties as early, early mid-season, late mid-season and late. Nevertheless, the weather conditions during the actual periods of ear emergence may cause a variation in a few days in this period and may prolong or cause unevenness in earing in a pure line. The earing data taken over a number of years with sowing at different times in the

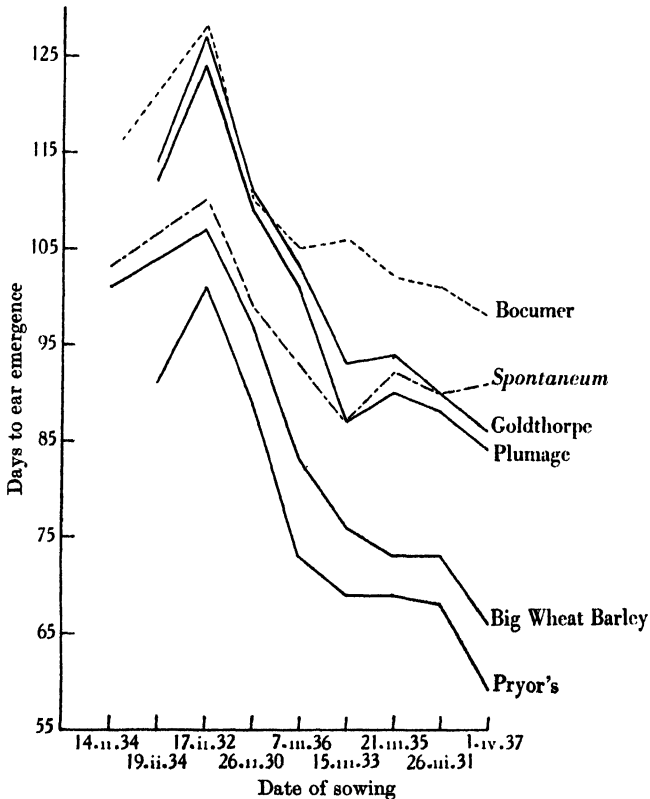


Fig. 1.

spring are given in Table I and Fig. 1. The important point to notice is, although earlier sowings generally mean a longer time from sowing to ear emergence, the differences in sowing time bear no relation to the differences in the date of ear emergence. Thus, a 2-day difference in the time of sowing in the years 1932 and 1934 was associated with considerable differences (up to 13 days) in the times taken for any one of the varieties to come into ear. On the other hand, in the years 1931 and 1933 an 11-day difference in the time of sowing entailed no difference in the

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time taken to ear emergence in some varieties, while the greatest difference was only 5 days.

Owing to the many uncontrolled differences in the seasons of the various years little else can be deduced from a study of these figures except the differential response of the varieties to the different times of sowing. Although the general tendency is to shorten the time from sowing to ear emergence as the sowing time becomes progressively later, it may be seen that, within the limits of the sowing times under review, this progressive shortening is not similar in each variety and as the sowing time becomes later some of the varieties show little reduction in the period to ear emergence. Examination of the figures shows that the

Table II. *Showing number of days from sowing to ear emergence with consequent decrease with successive sowings up to the time when earing becomes irregular and finally fails. The figures in brackets show the difference in days between the ear emergence of the variety in question, and that of Pryor's Chevallier*

(a) At Cambridge, England, 1932											
Variety	March			April		May		June		July	
	3	16	29	12	26	10	24	7	21	7	19
Pryor's Chevallier	87	76	67	58	48	39	37	32	32	33	32
Big Wheat Barley	97	86	75	63	54	47	41	41	39	40	40
	(10)	(10)	(8)	(5)	(6)	(8)	(4)	(9)	(7)	(7)	(8)
Goldthorpe	113	100	92	79	70	60	64				
	(26)	(24)	(25)	(21)	(22)	(21)	(27)				
<i>H. spontaneum</i>	97	87	82	81							
	(10)	(11)	(15)	(23)							
Bocumer	107	99	95	89							
	(20)	(23)	(28)	(31)							

(b) At Aberdeen, Idaho, U.S.A., 1931							
Variety	April			May			June
	8	20	30	10	19	30	8
Pryor's Chevallier	56	48	42	41	37	33	33
Big Wheat Barley	65	59	53	47	45	37	40
	(9)	(11)	(11)	(6)	(8)	(4)	(7)
<i>H. inter. transiens</i>	75	69	64	60	58	55	56
	(19)	(21)	(22)	(19)	(21)	(22)	(23)
Plumage	79	71	66	62	62	56	55
	(23)	(23)	(24)	(21)	(25)	(23)	(22)
Plumage-Archer	79	72	68	63	64	56	56
	(23)	(24)	(26)	(22)	(27)	(23)	(23)
Goldthorpe	83	74	69	68	68	54	69
	(27)	(26)	(27)	(27)	(31)	(21)	(36)
<i>H. parallelum</i>	77	76	64	58	58	51	50
	(21)	(28)	(22)	(17)	(21)	(18)	(17)
<i>H. spontaneum</i>	103	102					
	(47)	(54)					
Bocumer	107	102					
	(51)	(54)					

varieties with the shortest time to ear emergence are those which appear capable of the greatest reduction in the developmental phase to ear emergence, while in the later sowings the more slowly developing forms show very little, if any, reduction.

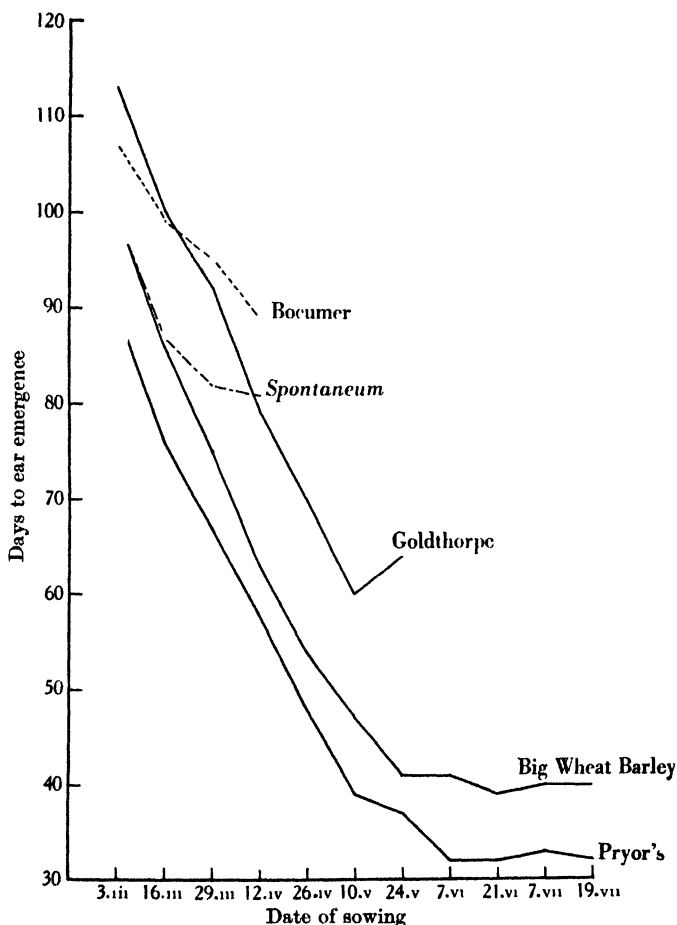


Fig. 2.

More exact evidence on the behaviour of varieties when sown at different times in the spring and summer may be found in Table II *a*, *b*, and Figs. 2, 3. In these two sets of data, successive sowings were made of certain varieties during two separate years, one in this country at Cambridge, and one at Aberdeen, Idaho, U.S.A. The progressive shortening of the period from sowing to ear emergence as the sowing

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time becomes later is easily discernible, although in the latest sowings this shortening may be no longer apparent in some cases. The distinctive behaviour of the early spring varieties, Pryor's Chevallier and Big Wheat Barley, the mid-season spring varieties, Plumage and Plumage-Archer, the late mid-season variety, Goldthorpe, and the winter varieties,

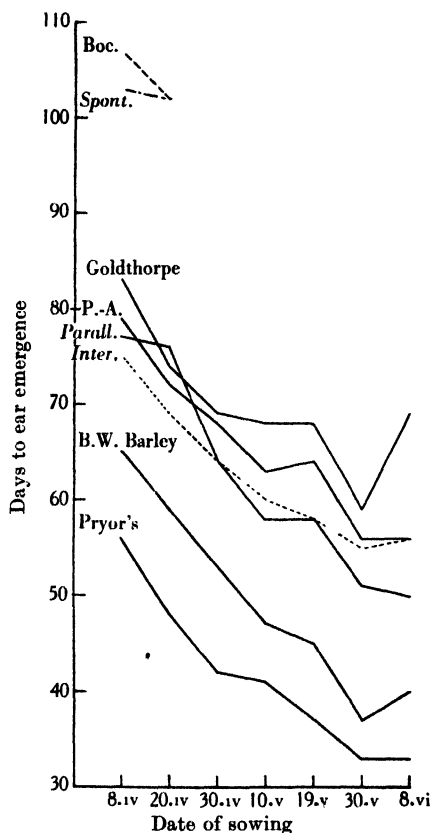


Fig. 3.

Bocumer and *H. spontaneum*, is clearly shown in these tables and figures.

It can also be seen that the amount of shortening of the life cycle from one sowing to the next is characteristic of each variety, and that the sowing date when there is no longer any shortening varies with the variety. When progressive shortening is no longer possible the earing becomes irregular and spread over a long period, and the times given in

the tables are those at which the first plant came into ear. Similar observations have recently been made for certain wheat varieties in Japan by Kakizaki & Suzuki (1937), who identify two critical times of sowing: (1) Critical sowing time for earliness, which is the sowing time showing the least number of days to ear emergence. (2) Critical sowing time for earing, which is the latest sowing time for ear emergence. These two critical dates vary with the characteristic spring or winter habit of varieties, and Kakizaki & Suzuki classify their varieties into seven groups according to their critical dates, and therefore also according to the intensity of their spring or winter habits. In extreme winter types the critical sowing times are the earliest, and with increasingly high expressions of the spring nature these critical sowing times become later, so that an early spring variety is characterized by later critical sowing times than a late spring variety, which may possess some degree of winter expression.

Kakizaki & Suzuki's conceptions for wheat are in general agreement with the results obtained in the present observations on barley. Pryor's Chevallier and Big Wheat Barley may be taken as examples of early spring varieties, Goldthorpe as a late spring variety, and *Hordeum spontaneum* and Bocumer as showing different expressions of the winter habit (Table II *a*). The varieties taken in this order show progressive intensification of the winter habit, and the characteristic behaviour with increasing lateness of sowing is obvious from the figures. In Table II *b* some other varieties which were used in the present hybridization experiments have been included. These tables will be referred to when the individual crosses are being studied, but there is one more important point requiring attention. The figures in brackets in the tables indicate the difference in earing time between the particular variety and Pryor's Chevallier when sown on the same date. It will be seen that these differences vary with the time of sowing when the winter varieties *H. spontaneum* and Bocumer are considered, being longer in the later sowings. The reason for this is that winter varieties cannot shorten their life cycle with progressively later sowings as spring varieties can, and although when sown early a winter variety may be classed as "early", when sown late it very quickly becomes a late variety or may fail to ear. This behaviour on the part of winter varieties is due primarily to the necessity of their being exposed to low temperatures during early growth before they can ear successfully. Early spring sowing may satisfy this need in some forms and early earing results. Later sowings may be partially successful, and the variety may ear considerably later, but very

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soon the critical sowing time for earing is reached with a consequent failure to come into ear.

The effect of low temperature exposure on the time taken to come into ear by a spring variety (Pryor's Chevallier) and a winter variety (Bocumer) may be seen in Table III and Fig. 4. In all cases grain which

Table III. *Number of days to ear emergence of a spring variety (Pryor's Chevallier) and a winter variety (Bocumer) when sown at different dates in the spring and subjected to low temperature grain pre-treatment before sowing*

	8 Mar. (field)	8 Mar. (glass- house)	15 Mar. (field)	22 Mar. (field)	29 Mar. (field)	5 Apr. (field)
Pryor's Chevallier control	81	63	72	67	60	56
Pryor's Chevallier pre-treated	80	60	71	66	60	56
Bocumer control	102	116	101	97	93	100
Bocumer pre-treated	99	96	92	87	83	83
Pryor's Chevallier (difference due to pre-treatment)	1	3	1	1	0	0
Bocumer (difference due to pre-treatment)	3	20	9	10	10	17

had been subjected to low-temperature pre-treatment before sowing was compared with untreated grain, and sowings were made successively, the first one in a glasshouse as well as in the field. Low temperature had little effect on Pryor's Chevallier, but it was very potent in reducing the time to ear emergence in Bocumer, except in the first sowing in the field where the low soil temperature had a similar effect to the artificial treatment before sowing. Thus, because spring varieties do not require this low temperature stimulation, and are stimulated to quicker development by high temperatures, whereas the winter varieties first require low temperature exposures, the difference in earing time between spring and winter varieties increases with lateness of sowing until the critical period of earing for the winter variety is reached. The effect of temperature is particularly clear in comparing the glasshouse and field sowings of the same date (8 March). The higher temperature of the glasshouse markedly decreased the time to ear emergence in the spring variety, and increased it in the winter variety.

The distinction between winter and spring varieties is, however, not clear cut. There are spring varieties which require no low temperature stimulation. Spring varieties are also very variable in the speed with which they come into ear, and in the range of sowing dates for successful earing, the later spring types merging into the forms which possess a weakly developed winter habit. These latter forms will ear normally

when sown early in the spring, but lose the capacity to shorten the life cycle with progressively later sowings before the late spring types. With

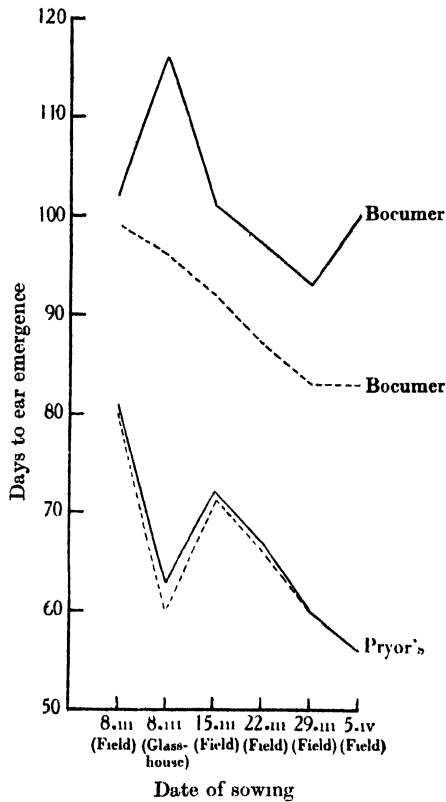


Fig. 4.

Solid line = control.

Broken line = treated.

increasing expression of the winter habit the critical time of sowing for earing becomes earlier and earlier in spring sowings, until the extreme winter types are reached which fail to ear within the period of ordinary spring sowings.

4. HYBRID MATERIAL STUDIED FOR INHERITANCE OF DATE
OF EAR EMERGENCE

The undermentioned nine crosses were studied in the present investigation:

- A. Big Wheat Barley \times Pryor's Chevallier.
- B. Pryor's Chevallier \times Plumage.
- C. Plumage-Archer \times Pryor's Chevallier.
- D. Big Wheat Barley \times Goldthorpe.
- E. *H. vulgare parallelum* \times *H. spontaneum*.
- F. *H. spontaneum* \times *H. intermedium transiens*.
- G. *H. vulgare praecox* \times B. 24.
- H (i). Pryor's Chevallier \times *H. spontaneum*.
- H (ii). Pryor's Chevallier \times Bocumer.

In all cases the material was sown in the spring on the grounds of the Cambridge University Plant Breeding Institute. The observations on each cross were not made in the same year, nor was the sowing on the same date in each year. The F_1 , F_2 and F_3 were sown in successive years, so that the successive generations cannot be regarded as being grown under identical conditions in so far as the sowing time and weather conditions differed in each year. From what has previously been said in this article, this is a serious defect in the genetic analysis of some of the crosses, but the susceptibility to growing conditions of some of the varieties was not realized when the investigations were commenced.

The behaviour and characteristics of each parent, and the procedure adopted in the handling of the hybrid progeny will be stated in each cross. In most cases the procedure was similar for each cross, but some modification was necessary in certain cases in the selection of material for growing on in the F_3 , owing to the amount of material available. The earing dates of the F_2 plants were recorded by inspecting the material each day and labelling each plant. At harvest each plant was pulled up and the material sorted according to the date of ear emergence. Owing to the death of a proportion of plants between earing and maturity, there was some loss in the field, and further loss of plants for F_3 observation resulted from the failure to set good grain or from the loss of ears. Where labels were still attached to plants at maturity the latter were included in the F_2 data, regardless of whether they possessed good ears or not. The large amount of material under observation precluded the possibility of sowing all the F_2 plants of some

crosses. It was therefore decided to include half the plants from each ear-emergence group, except in the case of only one plant falling in one group, under which circumstances that plant was always sown.

The amount of grain available for sowing from each F_2 plant varied with the cross. Where possible, sufficient grain to sow two ranks of twenty-three plants each was included, and the whole of the F_3 was sown at this rate of forty-six grains for each F_2 plant. In other cases sufficient grain for one rank only was available. The amount of material available in each cross and used in the observations will be stated in the discussion of the data given below.

The observations on the F_2 are in all crosses represented as solid line curves, with the parental earing curves included as broken lines, while in certain crosses the correlation between the earing time of the F_2 and F_3 has also been included.

The F_3 observations on some of the crosses are given as tables showing the earing behaviour of each culture. These tables are based on the F_2 classification in that the order given represents the grouping of the F_2 plants according to their time of ear emergence. Thus in passing from the first to the last culture in the table, increasing lateness of the corresponding F_2 plant, from which the F_3 culture was derived, is represented.

A. *Big Wheat Barley* \times *Pryor's Chevallier*

Pryor's Chevallier (*H. distichum nutans*) and Big Wheat Barley (*H. vulgare*) are two early spring varieties, the former being the earliest barley grown at Cambridge under all conditions of sowing, and the latter coming into ear 4–10 days later according to the time of sowing and the growing conditions. Pryor's Chevallier has a very wide range of sowing in the spring and summer, having come into ear normally when sown as late as the middle of July, while even when sown in the beginning of August the variety is still capable of earing, although very unevenly. The shortest period from sowing to ear emergence is achieved with sowings in the first and second weeks of July, when ear emergence commences 32–33 days after sowing. Later sowings lead to an increase in the time to ear emergence, but even so Pryor's Chevallier may be taken as the extreme expression of the spring type among the barleys used in these experiments.

Big Wheat Barley does not possess the capacity of Pryor's Chevallier for progressive shortening of the time to ear emergence with increased lateness of sowing, and therefore reaches the critical times for earliness

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and ear emergence before Pryor's Chevallier. The least number of days to ear emergence shown by Big Wheat Barley is with sowings made towards the end of June, when it comes into ear 39–40 days after sowing, while it has failed to ear with sowings after the third week of July. Therefore, although it must be classed as an early spring variety, Big Wheat Barley does not possess the extreme spring expression of Pryor's Chevallier.

The F_1 showed 50 % ear emergence 6–7 days after Pryor's Chevallier, which itself was 10 days earlier than Big Wheat Barley. There was, therefore, a tendency to the later parent on the part of the F_1 .

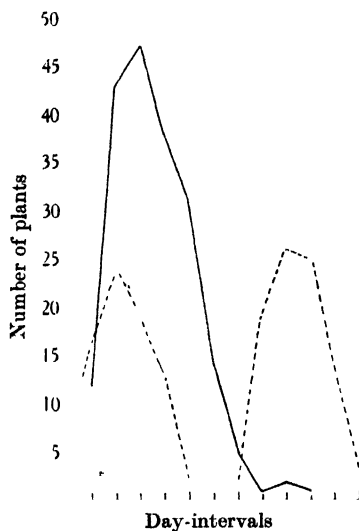


Fig. 5. F_2 Big Wheat Barley \times Pryor's Chevallier.

The ear emergence of the F_2 is given in Fig. 5. It will be seen that there is no indication of segregation, the curve tending to be a normal one, with its range lying within that of the parents. The earliest segregates commenced earing 1 day after Pryor's Chevallier commenced, and the latest segregates came into ear 2 days before Big Wheat Barley finished earing. The F_2 mode was reached 1 day after 50 % earing in Pryor's Chevallier, and over 95 % of the F_2 plants had come into ear before Big Wheat Barley commenced, the difference between the parental ear emergence being 7 days in this case. Therefore, in spite of the F_1 showing a tendency to the later parent, the F_2 inclined to the earlier parent, an inclination which would have been more marked if the parents had

differed by 10 days as they did in the F_1 sowing of the previous year. No attempt was made to sort the F_2 on ear type, i.e. six-row or two-row, etc.

The whole of the F_2 was sown at the rate of twenty-three grains per plant, there being ninety-two F_2 plants available. The first obvious characteristic of the F_3 is that certain of the earliest cultures gave plants which came into ear earlier than the early parent Pryor's Chevallier. There were, however, no plants later than Big Wheat Barley (Table IV).

Fig. 6 shows the correlation between the earing time of the F_2 plant and that of its F_3 culture. The time of ear emergence of the F_3 culture has been taken as the 2 days covering 50 % of ear emergence, and although

Table IV. F_3 Big Wheat Barley \times Pryor's Chevallier

Culture:	Date of ear emergence														
	17	18	19	20	21	22	23		25	26	27	28	29	30	31
1	1	2	4	6	4	3	.	.	.	1
2	2	.	.	8	6	3	.	.	1
3	.	2	1	3	.	4	.	.	.	1
4	.	1	7	3	2	2	.	1	1
5	4	4	4	4	.	1
6	2	8	2
7	1	6	2	2	2
8	.	.	.	3	.	1	1	4	5	4	3
9	3	2	8	2	.	1
10	1	3	5	.	3	3	2	1	.	.	.
11	5	5	1	.	.	2
12	2	10	9	.	3
13	4	10	5	1
14	.	.	.	1	1	12	3	.	.	1
15	.	.	.	4	4	5	4	1
16	1	9	5	4
17	1	2	6	9	2	.	2
18	.	.	.	5	4	6	1	1	.	.	1
19	1	1	4	4	3	1	1
20	3	8	4	2	2
21	2	3	5	6	4
22	1	5	5	.	2	.	.	1	.	.	.
23	.	.	.	3	2	1	6	4	2	4
24	.	.	.	4	5	6	4	.	.	1
25	7	1	1	.	.	.
26	4	2	5	5	.	2	3	.	.	.
27	3	2	5	5	.	3	1	.	.	.
28	1	4	3	11	.	1
29	2	2	3	2	5	1
30	6	1	8	2	4
31	1	1	3	3	.	2	1	1	.
32	3	4	3	3	.	3	1	1	.
33	1	1	12	2	1	2	.	.	.
34	3	1	5	4	2
35	2	5	2	7	1	1
36	4	3	4	4	1	.	.
37	5	5	5	2	1
38	.	.	.	1	4	6	3	4	.	1	.	2	.	.	.
39	3	3	4	4	1
40	6	7	4	3	.	2

Table IV (cont.)

Culture:	Date of ear emergence															
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
41	2	8	2	3	2	1	2	
42	2	6	5	1	4	.	.	1	.	.	.	
43	1	2	2	4	3	1	.	.	.	
44	.	.	.	2	1	10	1	1	3	
45	4	4	8	2	1	1	
46	2	6	2	3	2	.	1	1	.	.	
47	4	4	3	9	1	.	.	1	.	.	
48	2	.	5	5	5	.	2	1	.	1	
49	3	3	6	4	1	1	.	1	.	
50	1	.	1	2	4	2	5	3	1	1	
51	1	.	3	8	4	2	1	2	.	
52	1	.	.	5	5	5	1	1	2	.	
53	1	.	2	7	6	5	.	
54	2	2	6	5	1	
55	3	2	2	5	1	3	.	1	.	
56	2	5	3	1	2	7	.	.	.	
57	2	2	1	5	3	4	.	1	.	.	
58	6	2	3	2	2	1	.	1	2	.	
59	4	1	7	3	3	3	2	.	.	
60	2	2	2	2	5	2	1	.	.	
61	1	.	1	3	5	6	1	.	.	.	
62	1	3	4	7	3	
63	1	6	1	6	4	2	.	.	
64	1	4	5	1	3	2	1	.	1	2	
65	3	.	6	1	6	3	.	1	.	.	.	
66	1	2	4	1	7	2	.	1	.	.	.	
67	4	5	4	5	1	.	.	
68	.	.	.	1	.	8	3	2	3	1	
69	2	.	.	4	2	4	1	1	.	
70	5	2	4	4	2	.	.	
71	3	7	2	6	
72	1	4	5	2	.	2	.	
73	2	6	6	
74	3	4	6	3	2	.	
75	5	3	4	3	.	1	.	
76	1	2	.	2	4	
77	4	2	4	.	2	4	3	.	.	
78	6	9	2	2	3	.	.	
79	1	6	4	4	4	2	.	.	.	
80	1	7	4	4	.	1	2	.	.	.	
81	1	.	3	.	5	2	2	5	3	
82	3	1	13	2	
83	1	1	4	1	7	2	2	.	
84	1	2	2	2	1	6	1	4	.	.	
85	2	4	7	2	2	
86	1	3	4	3	4	1	4	.	1	.	
87	1	4	8	3	3	1	.	
88	1	1	3	6	1	4	.	
89	.	.	.	5	3	9	2	.	1	
90	1	.	4	3	6	1	2	.	.	
91	1	.	3	2	
92	.	.	.	3	6	6	4	.	.	.	1	
Pryor's Chevallier:	.	.	.	5	31	37	8	4	1	
Big Wheat Barley:	1	12	23	44	16	

this method gives no suggestion of the period of ear emergence of the cultures the close correlation is apparent except in the case of the latest earing F_2 plants, which in some cases show unexpectedly earlier earing in the F_3 . This may be partially explained on the assumption that these plants were in some way checked in their growth in the F_2 and therefore came into ear some days later than they should have if growth had not been inhibited. It does not appear, therefore, that there is any significance in the small peak apparent in the curve based on day to day



Fig. 6. Big Wheat Barley \times Pryor's Chevallier.

ear emergence, which suggests at first sight that the curve may be bi-modal.

The behaviour of each F_3 culture is given in Table IV. It will be seen that apart from the first five cultures, which are earlier than Pryor's Chevallier, there is very little suggestion of progressive lateness from the earliest to the latest cultures, nor is there any suggestion of discontinuity. Homozygous cultures appear to be distributed more or less evenly throughout the total F_3 , while those cultures which suggest heterozygosity do not show a very appreciable variability.

B. Pryor's Chevallier \times Plumage

Plumage may be taken as a typical mid-season two-row spring barley of the *H. distichum erectum* type. Spring sowings at Cambridge show it to be 18–25 days later coming into ear than Pryor's Chevallier. Unfortunately, no reliable data are available for its critical sowing dates owing to the failure of the 1938 observations due to drought. Nevertheless,

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the sowing observations at Aberdeen, Idaho, U.S.A., give some idea of its behaviour compared to Pryor's Chevallier (Table II *b*), whilst at Cambridge it may be taken to resemble Goldthorpe which, however, is a few days later, and probably reaches its limit of normal ear emergence before Plumage. At all events, in the normal spring sowings at Cambridge, Plumage appears to be capable of progressive shortening of the period from sowing to ear emergence with lateness of sowing, which leads to an average ear emergence of about 20 days later than Pryor's Chevallier.

The F_1 showed a 50% ear emergence exactly midway between the parents, being 12 days later than Pryor's Chevallier and 13 days earlier than Plumage.

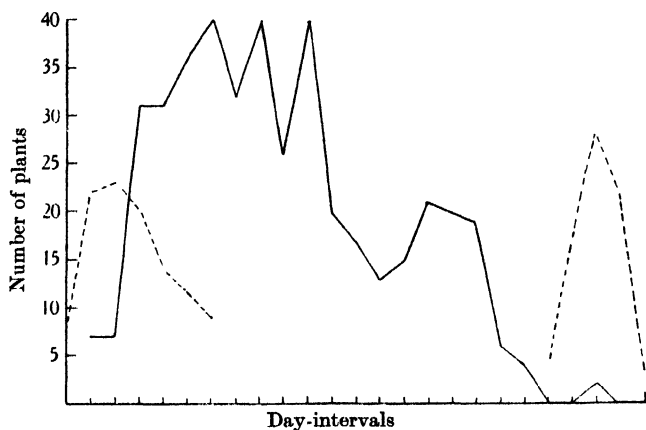


Fig. 7. F_2 Pryor's Chevallier \times Plumage.

The day to day ear emergence of the F_2 is given in Fig. 7. The range of ear emergence of the F_2 does not exceed the time from the commencement of earing of Pryor's Chevallier to the finishing of earing of Plumage. On the other hand 427 out of the 429 F_2 plants came into ear before Plumage commenced. The curve of the F_2 earing suggests a 3:1 segregation with earliness dominant, and the lowest point between the peaks occurs almost exactly half-way between the two parental 50% ear emergence dates. On the other hand, the 25% of apparently recessive forms come into ear before Plumage, with the exception of two plants, while the main peak of the curve is later than the earlier parent, there being no F_2 plants as early as the earliest Pryor's Chevallier plants nor as late as the latest Plumage plants.

The F_2 was approximately halved for the F_3 sowing, each F_2 group date being represented by half the plants except in the case of the

group being represented by one plant, in which case that plant was included in the F_3 . Each F_2 plant was sown at the rate of approximately forty grains.

The F_3 showed some plants earlier than Pryor's Chevallier and later than Plumage, thus demonstrating a somewhat greater range than the F_2 . The behaviour of each F_3 culture may be seen in Table V, and the high degree of correlation between the earing of the F_2 and F_3 in Fig. 8. The table of the F_3 cultures shows quite clearly the progressive lateness of these cultures based on the ear emergence of the F_2 plants from which they were derived, and the 174 cultures can be roughly divided into three

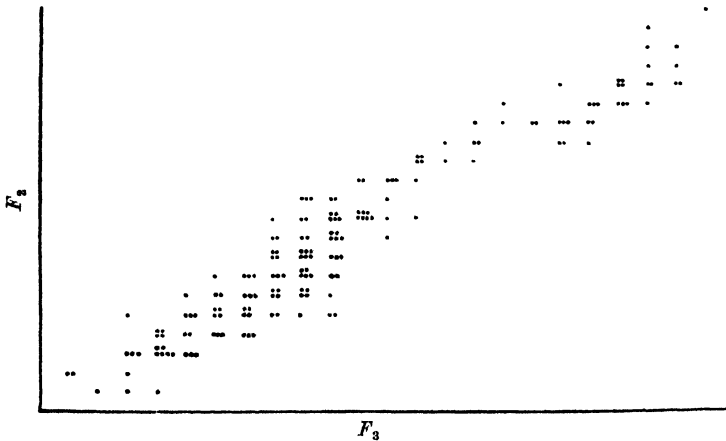


Fig. 8. Pryor's Chevallier \times Plumage.

groups based on the date of commencement, and the duration, of ear emergence. The first group, comprising roughly the first fifty cultures, is characterized by its earliness and relatively low proportion of heterozygous cultures, most of which do not have a very wide spread. The second group includes those cultures up to about number 124, and although the date of commencement of ear emergence of most of these cultures is very little later than the later cultures in the first group, there is a very much higher proportion of heterozygous cultures, most of which have a very wide spread or duration of emergence. The remaining cultures, which constitute the third group and are again roughly fifty in number, show a rapid increase in lateness and a lower proportion of heterozygous cultures, most of which do not have a long duration of emergence. It can be said, therefore, that the F_3 supports the theory of a single major factor difference which is suggested by the F_2 .

Date of ear emergence

[illegible]

Table V (cont.)

Culture:	Date of ear emergence															
	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4
91	2	1	4	2	5	5	1	3	2	1
92	.	.	.	1	2	.	1	2	4	3	6	6	4	2	1	1
93	.	.	.	3	3	3	1	3	3	3	7	8	4	1	3	2
94	.	.	2	1	2	.	1	2	6	5	5	5	7	1	1	5
95	2	4	2	3	4	10	4	7	2	1	3
96	2	2	2	4	4	4	3	7	3	1	1
97	3	1	1	4	5	4	3	7	3	1	1
98	.	1	.	.	3	1	1	1	3	1	6	3	5	2	4	3
99	1	1	5	1	.	6	3	7	3	1	1
100	.	.	1	1	.	1	1	1	1	4	6	3	1	2	4	1
101	.	.	1	1	1	1	1	1	1	3	7	6	3	3	5	2
102	2	2	5	2	7	2	3	2	4	4	1
103	.	.	1	4	2	2	2	2	3	2	2	3	1	4	1	2
104	1	.	1	3	.	2	7	2	4	1	1
105	1	.	.	2	1	3	3	5	4	3	5	1
106	2	1	2	2	8	6	3	2	1
107	2	2	1	1	5	3	6	3	1	2
108	2	3	2	3	3	9	7	6	2	4	1
109	.	.	.	1	1	1	1	3	2	3	1	6	9	2	1	2
110	1	1	2	1	3	5	6	5	2	3	2
111	3	1	5	5	5	2	2	1
112	2	.	.	6	1	5	7	5	2	3	3
113	3	1	3	4	4	1	2	4
114	6	1	3	4	1	6	3	3
115	.	.	.	1	.	.	1	.	3	1	5	11	1	2	2	4
116	.	.	1	1	.	.	1	2	2	2	4	3	6	4	1	1
117	1	.	7	4	2	5	4	2	2	1
118	1	1	.	2	3	3	7	8	2	1	1
119	1	1	.	6	4	2	2	6	2	1	1
120	.	.	1	1	1	1	1	1	2	8	3	2	2	3	1	5
121	.	.	1	1	1	1	2	2	3	1	5	5	4	1	6	1
122	.	.	.	1	1	1	2	3	2	3	3	3	1	5	2	2
123	1	3	2	1	3	3	3	1	2	1
124	1	1	8	2	2	1	1	12	11	14	3
125	1	.	.	1	1	1	6	2	2	3
126	2	1	1	2	1	1	1
127	3	9	.	3	7	6	4
128	1	3	2	4	3	2	1
129	4	3	1	6	3	3	2	1
130	1	2	4	1	5	7	2	5	4
131	1	1	1	2	3	3	11
132	1	1	2	4	4	2

[illegible]

C. Plumage-Archer × Pryor's Chevallier

Plumage-Archer is a similar type of barley to Plumage, but is generally 2–3 days later in ear emergence at Cambridge, where it has varied in being from 20 to 28 days later than Pryor's Chevallier. The general description of Plumage with regard to ear emergence and time of sowing may therefore be considered as applicable to Plumage-Archer and need not be repeated.

The F_1 showed a 50 % ear emergence exactly midway between the parents, being 12 days later than Pryor's Chevallier and 13 days earlier

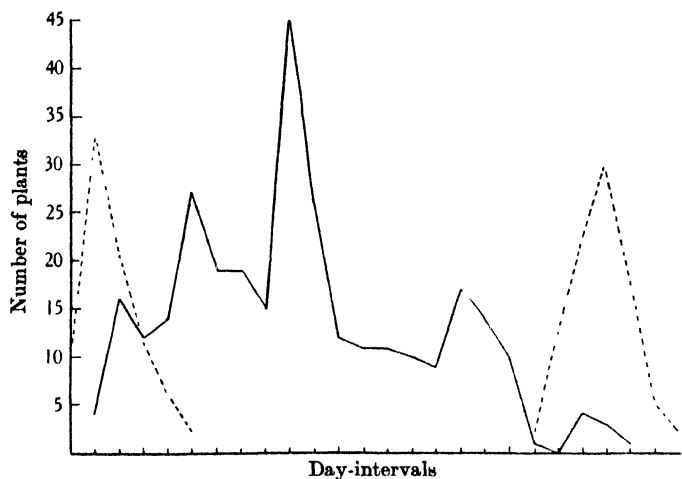


Fig. 9. F_2 Plumage-Archer × Pryor's Chevallier.

than Plumage-Archer. This corresponds identically with the F_1 of Pryor's Chevallier × Plumage.

The day-to-day ear emergence of the F_2 is given in Fig. 9. The range of ear emergence of the F_2 does not exceed the time from the commencement of earing of Pryor's Chevallier to the finishing of earing of Plumage-Archer, the earliest plants coming into ear when Pryor's Chevallier showed 50 % emergence, and the latest plants earing just before the latest plants of Plumage-Archer. On the other hand, 297 out of the 306 plants came into ear before Plumage-Archer commenced. The day to day ear emergence gives a curve which approximates well to a 1 : 2 : 1 segregation, but the 2-day grouping suggests more obviously a 3 : 1 ratio with earliness dominant and the lowest points between the peaks occurring nearer the later parent, and not midway between the parental 50 % ear emergence

dates. On the other hand, the main peak is later than the earlier parent and the subsidiary peak earlier than the later parent, but there is a minor peak corresponding with the latter.

It may be seen, therefore, that there are certain differences between the F_2 characteristics of this cross and the F_2 Pryor's Chevallier \times Plumage, although both conform to a 3 : 1 ratio with dominance of earliness. In the first place the main peak of the Pryor's Chevallier \times Plumage-Archer F_2 is considerably later reaching a maximum, and the peak is considerably more irregular. Secondly, the break between the main peak and the subsidiary peak is not so distinct and the lowest point is not midway between the two parents, but is later. Thirdly, the minor peak associated with the later parent is more distinct. It is probable that all these characters tending towards the expression of increased lateness in the F_2 are associated with the somewhat later ear emergence of Plumage-Archer compared with Plumage.

The F_3 observations were obtained in a similar manner to that in the Pryor's Chevallier \times Plumage cross. In the present case no plants earlier than Pryor's Chevallier or later than Plumage-Archer were obtained, but the F_3 showed a slightly greater range than the F_2 , as was the case in the Pryor's Chevallier \times Plumage cross. The F_3 suggested much the same state of affairs as was described for the Pryor's Chevallier \times Plumage cross, although perhaps less obviously, and may be said to support the theory of a single major factor difference suggested by the F_2 .

D. *Big Wheat Barley* \times *Goldthorpe*

Goldthorpe is a late mid-season two-row variety of the *H. distichum erectum* type. It is later than either Plumage or Plumage-Archer and probably has a shorter period of successful spring sowing. The characters of Big Wheat Barley have been described in the first cross, and the relative difference between it and Goldthorpe may be seen from Tables I and II. Although with normal spring sowings at Cambridge, Goldthorpe is about 14–17 days later than Big Wheat Barley, differences as small as 10 days and as large as 23 days have been observed.

The F_1 was intermediate, coming into ear 5 days after Big Wheat Barley and 12 days before Goldthorpe, thereby showing a distinct tendency to the earlier parent.

The F_2 was too small for a thorough examination of this cross, only 115 plants being labelled at ear emergence. The earing behaviour of this F_2 is, however, of sufficient interest to warrant description, and the day-to-day emergence is given in Fig. 10. The smallness of the population

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prevents an accurate analysis of the segregation, but a 3 : 1 ratio with dominance of earliness can be visualized, if the curve based on 2-day grouping is broken midway between the two parents, or a 1 : 2 : 1 segregation could be applied to the day-to-day earing data. The 2-day grouping, however, indicated that a 3 : 1 segregation is the more accurate, but in neither case is the evidence for a single major factor difference very convincing.

The most interesting characteristic of this segregation is, however, that there are F_2 segregates considerably earlier than the early parent, and 25 % of the plants have come into ear by the time the early parent has reached 50 % ear emergence. The tendency of the F_1 to the early parent indicated a stronger dominance of the earliness in this cross, and the F_2 manifests this, not in "shift" of the peak of the F_2 dominants, but in the segregation of earlier types. On the other hand, no greater

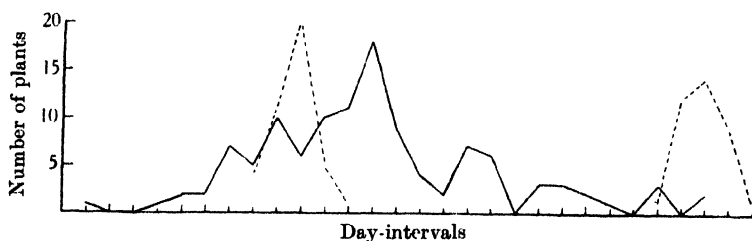


Fig. 10. F_2 Big Wheat Barley \times Goldthorpe.

proportion of the segregates come into ear before the later parent than in the two crosses described previous to this one. The behaviour and characteristics of the parents give little indication of the segregation of these early F_2 types, in fact it might have been expected that the tendency would have been towards the later parent.

The whole of the F_2 was sown at twenty-three grains per plant. The F_3 range was no greater than that of the F_2 , but plants later than the later parent, as well as earlier than the early parent, were observed. The appearance of the plants later than the late parent was partly due to the earlier sowing of the F_3 in 1934 than of the F_2 in 1933, so that the late parent came into ear earlier with the F_3 , while the latest plants in the F_3 were also somewhat later than those of the F_2 . The transgressive nature of the F_2 was borne out by the F_3 , in which there was a considerable number of plants earlier than the early parent, and at least one culture homozygous for transgressive earliness. But whereas in the F_2 there was no transgression beyond the later parent, there were four F_3

cultures suggesting homozygosity for transgressive lateness. It must be remembered, however, that there was a month's difference in the sowing times of the F_2 and the F_3 , and there was a greater difference in the earing times of the parents with the later sowing of the F_2 than with the earlier sowing of the F_3 . This increased difference was due to the greater lateness of the later parent (Goldthorpe), which, as stated above, shows a greater development of the winter habit than the normal mid-season varieties as exemplified by Plumage and Plumage-Archer.

The F_3 could not be as clearly separated into the three groups which characterized the two previous crosses, and it cannot be said to support the suggested 3 : 1 ratio of the F_2 , which, however, is not as obvious as in the two crosses just mentioned. There was a larger proportion of heterozygous cultures with a wide range of ear emergence in this cross, and these occur among the earlier cultures. There was, however, a marked increase in lateness with the latter part of the table, with an accompanied decrease in the range and proportion of heterozygotes. The whole table suggested a discontinuity in the behaviour of the F_3 cultures which is not apparent in the other crosses so far described.

E. *H. vulgare parallelum* \times *H. spontaneum*

H. vulgare parallelum is an early earing six-row form as may be seen from Tables I and II. It is not as early as Big Wheat Barley, but is earlier than any two-row variety except Pryor's Chevallier, and has a late critical period of sowing for ear emergence.

H. spontaneum, on the other hand, is distinct from any form yet described. It is a winter variety, which can be sown in the spring, but has a narrow range of sowing time for successful ear emergence. When sown in the early spring (early February), *H. spontaneum* is practically as early as Big Wheat Barley, but it rapidly becomes a late ear-emerging variety as sowing time becomes later, and very quickly fails to ear (Tables I and II). February sowings usually ensure earliness, while sowings towards the end of March lead to lateness with a consequent failure to ear in sowings after the second or third week of April.

The significance of this behaviour is that *H. spontaneum* may ear before *H. vulgare parallelum* with early sowings, and after *H. vulgare parallelum* in later sowings, the difference between the two varieties varying considerably. Thus in Table I, the three February sowings show *H. spontaneum* to be earlier by 9, 7 and 3 days respectively, while in the four March sowings it is later by 1, 5, 7 and 7 days respectively. The single April sowing leads to a great increase in lateness, so that *H. spon-*

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taneum is 16 days behind *H. vulgare parallelum*. It can be seen that under certain conditions these two varieties may ear on the same day.

Unfortunately the F_1 was not available for ear emergence observations, but the F_2 sown on 21 March is shown in Fig. 11, in which it may be seen that *H. spontaneum* is the later parent by 5 days. There is no suggestion of a simple segregation, and the most obvious characteristic of the F_2 is its transgressive nature with a great preponderance of forms earlier than either parent. The smallness of the population makes any critical analysis of the F_2 impossible.

The whole of the F_2 was sown at the rate of twenty-three grains per plant. This sowing was made on 21 February and *H. spontaneum* was

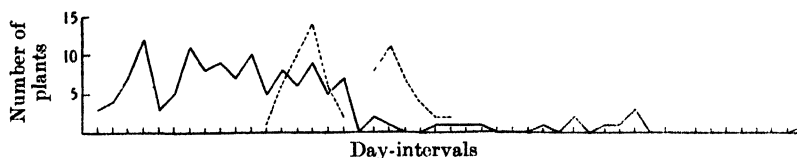


Fig. 11. F_2 *H. vulgare parallelum* \times *H. spontaneum*.

8.9 days earlier than *H. vulgare parallelum*. The strong correlation between the F_2 and F_3 breaks down with the later cultures as would be expected with the considerably earlier sowing of the F_3 compared with the F_2 . This, of course, suggests that if the F_2 had been sown in February, the very late cultures would not have been apparent and the curve would have been considerably modified. Very little can be interpreted from the F_3 , which strongly suggests discontinuities, and is more complicated than in any of the previous crosses.

F. *H. spontaneum* \times *H. intermedium transiens*

H. intermedium transiens is a botanical type which is intermediate between the true six-row barleys and the two-row barleys, in that the lateral spikelets set varying amounts of small grain, whereas in the true six-row the laterals are all fertile and in the two-row the laterals are staminate. *H. intermedium transiens* is an early mid-season variety coming into ear a little earlier than Plumage-Archer and Plumage, and a little later than *H. vulgare parallelum*, the behaviour of which has been described in previous crosses (see Tables I and II).

H. spontaneum has been described in the cross *H. vulgare parallelum* \times *H. spontaneum*, and it is only necessary to stress the fact that the variety may be earlier than *H. intermedium transiens* when sown early, and later when sown at a date after the middle of March, while the two

varieties may ear simultaneously when sown about 15 March. It might be mentioned that *H. spontaneum* and *H. vulgare parallelum* show simultaneous earing when sown around 7 March, so that in the present cross it is to be expected that increased lateness will be evident in the F_2 segregation.

The F_1 earing time was not observed, but the F_2 is given in Fig. 12. The whole of the material was sown on 22 March and it will be seen that at this date *H. spontaneum* is slightly the later parent. The F_2 resembles that of *H. vulgare parallelum* \times *H. spontaneum* in showing very marked transgressive segregation, but in the present cross there is a greater proportion of later types. This is to be expected, as stated above, owing to the later habit of *H. intermedium transiens* as compared with *H. vulgare parallelum*.

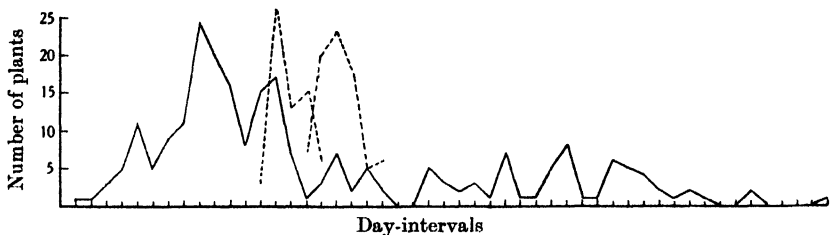


Fig. 12. F_2 *H. spontaneum* \times *H. intermedium transiens*.

The F_2 population of the *H. spontaneum* \times *H. intermedium transiens* cross can be made to fit a 3 : 1 ratio very accurately, with earliness dominant. It can be seen, though, that such a segregation bears little relation to the ear emergence of the parents, and is very improbable, the 25 % of "recessive" forms coming into ear after the later parent had finished emergence. The long drawn out emergence of these late types is similar to the previous *H. spontaneum* cross, and is presumably due to the lateness of the sowing, because such excessively late types did not appear in the F_3 , which was sown a month earlier in the following year.

The behaviour of the F_3 cultures is given in Table VI, and the F_2 - F_3 correlation in Fig. 13. The transgressive nature of the segregation is borne out by the F_3 , but as mentioned above the excessively late types were not recovered, and the F_2 - F_3 correlation therefore broke down with the late segregates which came into ear after 10 June. It should also be mentioned that in the F_3 sowing *H. spontaneum* was the earlier parent by 10 days. As in the previous cross involving *H. spontaneum* the F_3 is complex and strongly suggests discontinuities. The possibility

Table VI (cont.)

Culture:

[illegible]

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of a single major factor difference was mentioned from observations on the F_2 , but this hypothesis was stated to be improbable. The F_3 gives

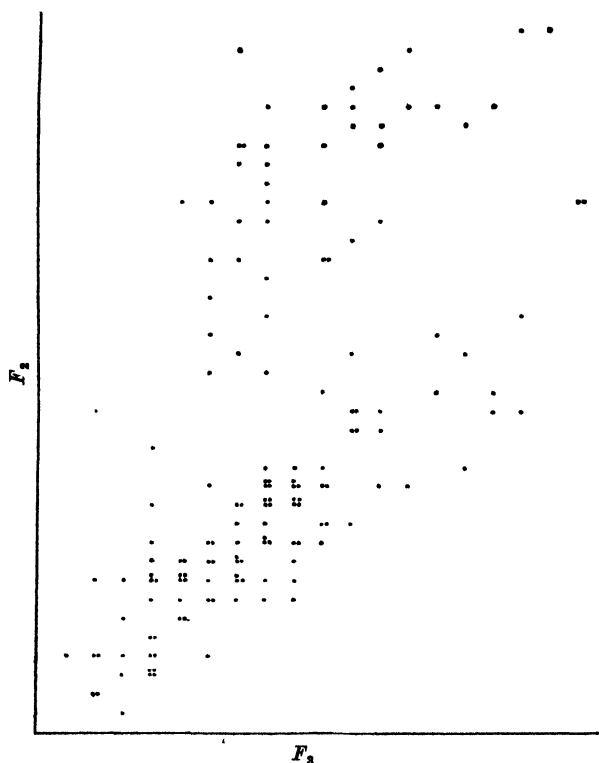


Fig. 13. *H. spontaneum* \times *H. intermedium transiens*.

further evidence of a greater complexity, and it may be assumed that it is inaccurate to interpret the F_2 on a 3 : 1 basis.

G. *H. vulgare praecox* \times B. 24

Both of these parent barleys are six-row *H. vulgare* types, which, however, differ considerably in their ear emergence characteristics. Unfortunately full data are not available for these two forms, but reference to Table I will indicate the most important points. *H. vulgare praecox* is an early mid-season variety; B. 24, on the other hand, is a winter variety which is late in all spring sowings and cannot be sown successfully in the spring later than the end of March. On the 1938 sowings, B. 24 failed to ear after a sowing on 4 April, even a sowing of

4 days later showing no tendency to ear, while in the 4th April sowing only one plant emerged.

The F_1 ear emergence was not observed. The day-to-day ear emergence data of the F_2 are given in Fig. 14. These show that the segregation can be interpreted on a 3 : 1 ratio basis with the break in the curve occurring at the mid-point of the total F_2 range, but not midway between the earing dates of the parents. Owing to the lateness of sowing of the F_2 and the parents (22 March), the 25 % of late plants shows a very extended ear emergence, and B. 24 is 33 days later than *H. vulgare praecox*. The earliest F_2 segregates came into ear earlier than the early parent, while

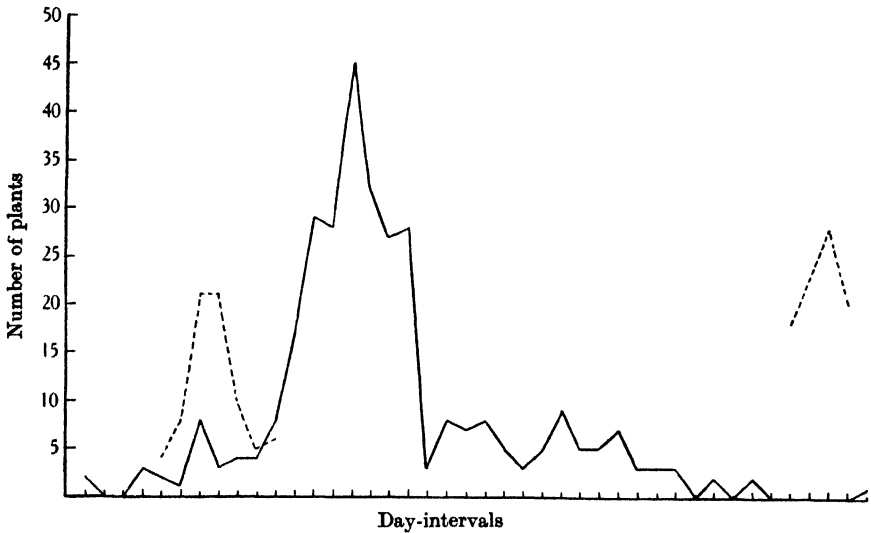


Fig. 14. F_2 *H. vulgare praecox* \times B. 24.

all the plants, with the exception of one, had emerged before the later parent. There is thus a transgression towards the early parent only.

Only half the F_2 was sown for F_3 observations and, owing to the F_3 sowing being one month earlier than the F_2 sowing, B. 24 was later than *H. vulgare praecox* by 21 days instead of 33 days as in the F_2 . There is not the range of earing in the F_3 that was apparent in the F_2 , but the segregation earlier than *H. vulgare praecox* was again apparent. In spite of the difference in sowing times of the F_2 and F_3 , there was a high correlation even between the earing dates in the later cultures (Fig. 15). This differs from the *H. spontaneum* crosses and is due to the earing characteristics of B. 24, which possesses a stronger expression of the

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winter habit, and never behaves as an early barley when sown in the early spring, or even in the winter. The F_3 does not show the more obvious discontinuities of the *H. spontaneum* crosses, but on the other hand cannot be said to support the single major factor difference

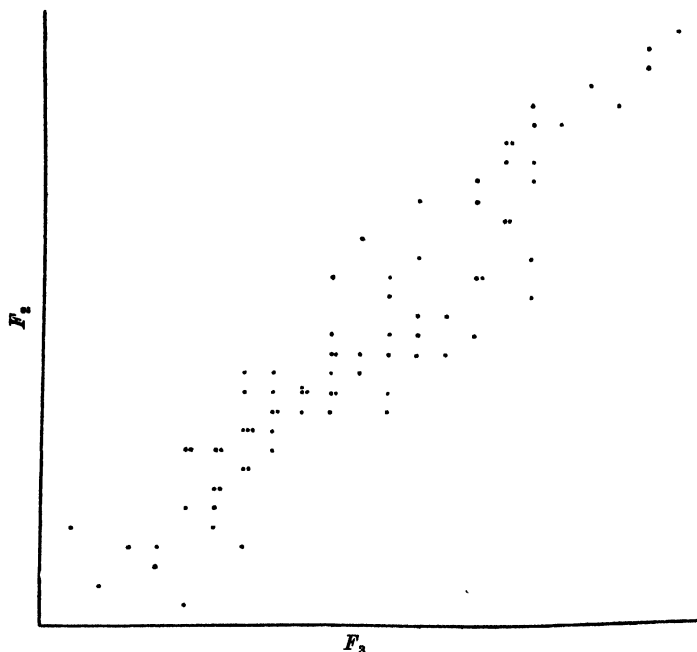


Fig. 15. *H. vulgare praecox* \times B. 24.

suggested by the F_2 type of curve, but not supported by the transgressive segregation. There is some suggestion of an aggregation of the heterozygotes of the F_3 in the middle cultures of the table, but these cultures do not show the spread that characterized the similar cultures in the two crosses which suggested more strongly a single major factor difference.

H. *The effect of time of sowing on the time of ear emergence of two hybrid progenies*

In order to illustrate the significance and importance of the time of sowing in studying the inheritance of the time of ear emergence, two crosses were made, and the progenies observed when sown at different dates. In both cases the crosses were between two markedly contrasting types with regard to ear emergence and therefore only illustrate the behaviour of such divergent types.

(i) *Pryor's Chevallier* \times *H. spontaneum*

Both of these varieties have been described in previous crosses, and their characteristics need not be referred to again. The hybrid grain was divided into six lots, each of twenty-two grains, and sown with the parents on the following dates: 25 March, 8 April, 22 April, 6 May, 20 May, 6 June. These sowings are later than would have been desirable for the experiment, but the conditions of the soil were such as to prevent earlier dates.

H. spontaneum succeeded in coming into ear only in the first sowing, and it was 30 days later than *Pryor's Chevallier*. The F_1 showed regular

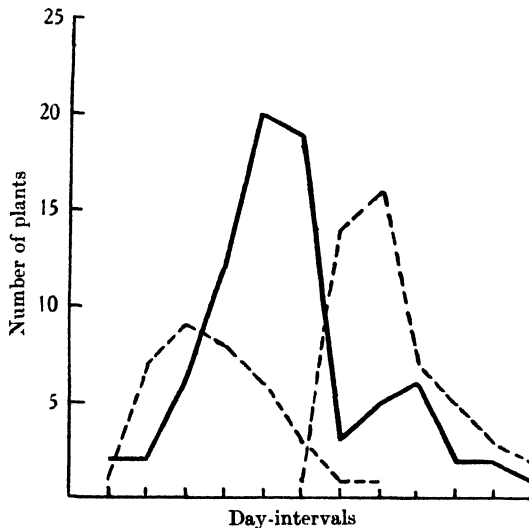


Fig. 16. F_2 *Pryor's Chevallier* \times *H. spontaneum*.

earring in the first two sowings only, and then emerged 4 and 5 days respectively after *Pryor's Chevallier*. In the third and fourth sowing the F_1 earing was irregular, and started 14 and 43 days respectively after *Pryor's Chevallier*. No ear emergence of the F_1 occurred in the fifth and sixth sowings. This experiment shows clearly, therefore, how in certain types of crosses the time of sowing can affect the F_1 behaviour.

The F_2 was halved and sown in the following year, and two widely separate dates were chosen, e.g. 8 February and 3 April. The F_2 and parental earing dates for these two dates are given in Figs. 16 and 17. In the earlier sowing the parents reached their maxima 5 days apart, but they overlapped. The F_2 commenced earing with *Pryor's Chevallier*,

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and finished with *H. spontaneum*, showing a bimodal 3 : 1 segregation. The minor peak coincided with the later parent.

In the later sowing there were 30 days between the parental 50 % ear emergence dates. The segregation in this case is approximately

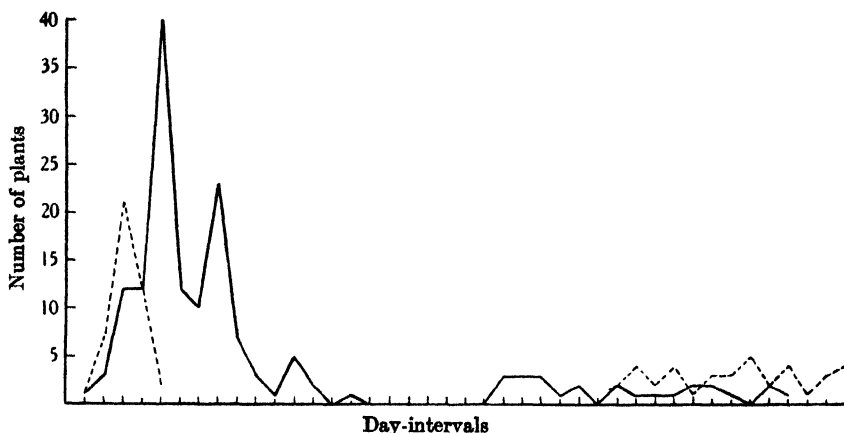


Fig. 17. Pryor's Chevallier \times *H. spontaneum*.

5.5 : 1, and the distinction between the two peaks of the curve is more pronounced than in the earlier sowing. The other marked difference between the two sowings is the much greater range of the F_2 earing, and the much accentuated protraction of the earing of the late types.

(ii) *Pryor's Chevallier* \times *Bocumer*

Bocumer is a six-row *H. vulgare* winter type, which is late coming into ear with all spring sowings and has a critical sowing date for ear emergence at Cambridge towards the end of the second week in April, although it has failed to ear with sowings in the first week. It has not the characteristic of being an early barley when sown in February, which is so marked in *H. spontaneum*, and is invariably later than that variety. Bocumer varies from 15 to 39 days later in ear emergence time than Pryor's Chevallier according to the time of sowing.

The hybrid grain was sown on the same six dates as for the previous cross, but unfortunately these were too late for the best results. The F_1 plants came into ear irregularly in the first two sowings, and failed to emerge in the remaining four. The approximate dates of emergence of the first two sowings were 17 and 20 days respectively after Pryor's

Chevallier. Bocumer failed to emerge in all sowings. Therefore, as in the previous cross, the sowing date affected the F_1 ear emergence.

The F_2 was divided into two, and sown with the parents on 8 February and 3 April as previously described. The earliest segregates in the February sowing commenced to ear when the early parent was at its maximum, and the latest plants had come into ear before Bocumer had commenced (Fig. 18). The segregation was indistinctly bimodal,

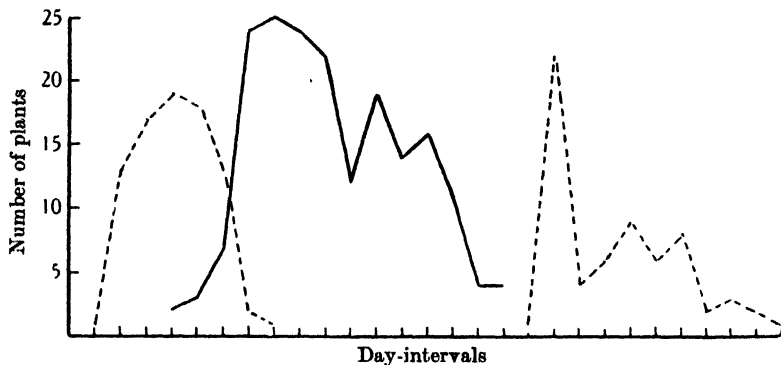


Fig. 18. F_2 Pryor's Chevallier \times Bocumer.

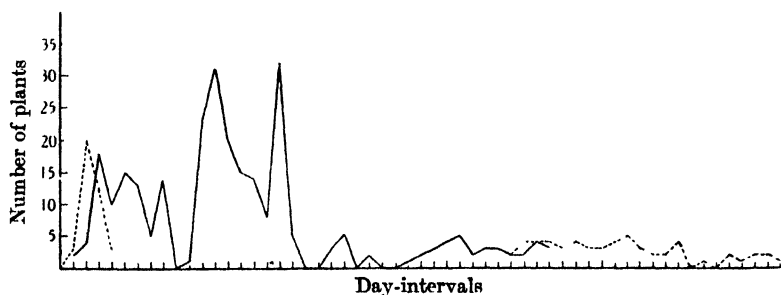


Fig. 19. F_2 Pryor's Chevallier \times Bocumer.

suggesting a 2:1 ratio if any is to be applied. The F_2 from the April sowing was quite distinct from that of the February sowing (Fig. 19). Although the parents were approximately 40 days apart in their earing dates in this sowing (contrasted with 18 days in the February sowing), the F_2 commenced one day before the early parent was at its maximum and finished just after the late parent commenced. The behaviour of the earliest segregates was thus similar in the two sowings, but the later segregates overlapped the late parent in the April sowing, but did not do so in the February sowing.

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The main features of the segregation in the two sowings were, however, quite distinct. The F_2 ear emergence of the April sowing shows at least three distinct sections to the curve, which is in no way comparable to the February sowing. No simple type of segregation can be recognized in the later sowing, and it has not served to elucidate the peculiar and indistinct behaviour of the early sowing. This experiment, however, agrees with the previous one in illustrating the marked effect of time of sowing on the character of the F_2 segregation in a study of the inheritance of time of ear emergence in certain crosses.

5. DISCUSSION AND CONCLUSIONS

From the evidence offered by the crosses described in this paper, it seems obvious that the only hereditary character which is common to all is a tendency to the dominance of earliness of ear emergence. This is expressed in relation to the F_2 population considered independently of the parents, because the dominance of the F_2 segregates may bear little relation to the dominant parent when judged on the one year's observations. But in so far as the majority of the F_2 segregates are early in relation to the minority, it may be said that earliness is the dominant character.

The actual expression of this dominance, both in relation to the proportion of early segregates to late segregates and in relation to the earing of the parents, varies with the parents used in the various crosses, and with the time of sowing of the F_2 population. There is little doubt that the gradation from the early spring forms to the late earing true winter forms in cereals includes a large number of physiological types differing in their response to environmental conditions in relation to their date of ear emergence. Therefore, earliness or lateness in ear emergence, as observed under one set of conditions, may not give a true measure of the physiological differences between varieties, while simultaneous ear emergence is not necessarily a criterion of identical physiological character. In other words, ear emergence studies are apt to be concerned with phenotypic, instead of genotypic, differences.

The results obtained by the observations on the crosses described in this paper indicate that the diverse results obtained may be explained to some extent by the different physiological characteristics of the parents in relation to their particular response to the time of sowing. This means, of course, the effect of the two most important environmental factors, viz. photoperiodic exposure and temperature, on the phasic development

of the plants. The research work conducted by other investigators on this important problem indicates that there are many physiological types of cereals, but the simplest expression is in relation to the relative degrees of the spring and winter habits, which manifest themselves characteristically under different conditions of growth, in so far as the two main environmental factors differ. The application of these principles to the crosses here under consideration may now be briefly reviewed.

A. Big Wheat Barley \times Pryor's Chevallier

The parents here represent two similar physiological types, resembling one another very closely in the expression of their ear emergence dates in response to different times of sowing. Both varieties are early spring forms with a late critical sowing date for ear emergence, but Pryor's Chevallier possesses the higher expression of the spring habit in that it is earlier, and has later critical sowing times. The lack of any apparent segregation and the intermediate earing of the F_2 is apparently indicative of the close physiological similarity of the two parents with regard to the major factors controlling the date of ear emergence. On the other hand, the F_2 earing characteristics, and the correlation between the F_2 and the F_3 show that there are minor hereditary differences apparently of a "quantitative" nature, but which cannot manifest any obvious segregation under the growing conditions.

*B and C. Pryor's Chevallier \times Plumage and
Plumage-Archer \times Pryor's Chevallier*

These two crosses may be considered together, as they illustrate similar parental combinations, although indicating minor differences, with regard to the later parents, which are to some extent reflected in the F_2 's. Both Plumage and Plumage-Archer are spring varieties with mid-season earing, with Plumage-Archer the slightly later form. Compared with Big Wheat Barley, both these mid-season varieties must be considered to have a higher expression of the winter habit, and their earing behaviour under late sowing conditions bears out this supposition. The difference in earing time between Pryor's Chevallier and Plumage and Pryor's Chevallier and Plumage-Archer is considerably greater than between Pryor's Chevallier and Big Wheat Barley, and their capacity for progressive shortening of the life cycle with increased lateness of sowing is considerably less in the mid-season varieties than in the early varieties.

The F_2 segregation of the two crosses gives a very strong indication of a 3 : 1 ratio with dominance of earliness, and the F_2 ranges do not

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exceed the time occupied by the first plants of the early parent and the last plants of the late parent to come into ear. Nevertheless, in both F_2 populations practically all the plants had come into ear before the late parent, and there were very few plants as early as the early parent. Therefore, it cannot be said that the two segregating types of the F_2 are genotypically or phenotypically similar to the parents, and although it may be true to say that in both cases the parents differ by one major ear-emergence factor, such a statement does not give a complete indication of the genetical differences, even judged on the F_2 behaviour and confirmed by the F_3 .

It is interesting to notice, also, that the small difference in the ear emergence behaviour of Plumage and Plumage-Archer, as exemplified by the slightly later character of the latter variety, is reflected in the F_2 . In the Pryor's Chevallier \times Plumage-Archer cross, the F_2 is slightly later in relation to Pryor's Chevallier than in the Pryor's Chevallier \times Plumage cross. This indicates either a lower concentration of the dominant factor in Plumage-Archer than in Plumage, or else the occurrence of later modifying factors.

D. *Big Wheat Barley* \times *Goldthorpe*

This cross resembles the two previous ones in the dominance of earliness, but although there was perhaps a superficial resemblance to a 3 : 1 F_2 segregation, the occurrence of transgressive earliness and the behaviour of the F_3 do not substantiate a single major factor difference. The occurrence of transgressive earliness is interesting in this cross involving two spring forms, but there is evidence to suggest that Goldthorpe possesses a stronger development of the winter habit than the other mid-season spring varieties (Plumage-Archer and Plumage) in these investigations. One therefore has to visualize Goldthorpe as a physiological type intermediate between the Plumage type and the *H. spontaneum* type, but tending more to the former. The F_2 supports this theory, resembling to some extent the F_2 's of the Plumage-Archer and Plumage crosses, but showing a weak expression of the transgression which so strongly characterizes the *H. spontaneum* crosses.

E. *H. vulgare parallelum* \times *H. spontaneum*

The F_2 of this cross showed no evidence of a simple segregation, and the most striking characteristic was the very marked transgressive segregation beyond both parents. This was particularly marked in the early forms, and the dominance of earliness is here extreme in its

expression. It has been pointed out that probably much of the peculiar F_2 behaviour can be traced to *H. spontaneum* which is itself peculiar in its response to the time of sowing, possessing as it does a characteristic development of the spring-winter balance. Owing to the susceptibility of *H. spontaneum* in the fluctuation of its time of ear emergence with time of sowing, it also follows that the type of segregation will vary with the sowing time, as has been shown in another experiment involving this form. This cross may be taken as an illustration of the impossibility of assessing the genotypic constitution of a variety, in relation to the time of ear emergence character, by observations under one set of conditions. It also emphasizes how phenotypic similarity between two forms may be accompanied by striking genotypic differences under certain conditions, with a consequent complexity in the F_2 progeny. It would, of course, be a simple matter to give a genetic explanation of the occurrence of the marked transgression in this cross by assuming that the two distinct physiological parental types can be represented by the notation **AA bb** and **aaBB**. The segregation of the two types **AABB** and **aabb** would consequently give the transgressive types.

F. *H. spontaneum* \times *H. intermedium transiens*

This cross has much in common with the previous one, and much that has been stated above is therefore applicable here. The peculiar behaviour of *H. spontaneum* is probably responsible for the great transgressive segregation, which in the present cross can, however, be identified with a 3 : 1 ratio. It is manifest, however, that it would be quite inadequate to ascribe a single factor difference between *H. spontaneum* and *H. intermedium transiens*. The obvious discrepancy between the F_2 and the two parents and the characteristics of the F_3 precludes any such simple interpretation being applied, and indicates how misleading would be any such statement to the effect that a single factor difference is applicable. The transgressive segregation can be explained in this cross as for the previous one.

In both crosses E and F it is obvious, from what has been stressed continuously in this paper, that a clearer indication of the hereditary behaviour might have resulted if the F_2 had been sown at a different time from that which is being discussed. The interpretations here given are only applicable under the conditions of the present observations.

G. *H. vulgare praecox* × B. 24

The parents here represent an early mid-season variety and a variety exemplifying as high an expression of the winter habit as any utilized in these experiments, Bocumer being the only comparable variety. It is therefore interesting that the F_2 segregation should suggest a single major factor difference, but with some transgression, there being little suggestion of the peculiar F_2 behaviour characterizing the crosses involving the spring-winter *H. spontaneum*. The results obtained from this *H. vulgare praecox* × B. 24 cross are to some extent similar to those obtained from crossing the early varieties Pryor's Chevallier and Big Wheat Barley with the mid-season varieties Plumage, Plumage-Archer, and Goldthorpe, except that in the former case the late recessive forms are very protracted in their ear emergence. This may be due to the unduly late sowing of the F_2 , whereby B. 24 is reaching its critical sowing time for ear emergence.

In the crosses studied in these experiments a certain amount of evidence for a single major difference has been found in crosses involving the following types: early × mid-season, early × late mid-season, early mid-season × late (winter). In each case the parents represent stable forms with regard to time of ear emergence and time of sowing, in so far as the relative dates of ear emergence are predictable regardless of the sowing time. But only in the two crosses Pryor's Chevallier × Plumage and Plumage-Archer × Pryor's Chevallier was the F_2 strongly in support of this hypothesis and also supported by the F_3 . The other crosses in which the F_2 showed a curve approximating to a 3 : 1 ratio were also characterized by varying degrees of transgressive inheritance, while the F_3 did not support the single major factor difference. *H. vulgare praecox* × B. 24 comes in this latter category, and as has been stated before involves the hybridization of two distinct physiological types—a spring type and a winter type.

H. *The effect of sowing time on the ear emergence of hybrid progenies*

Although in many types of crosses the time of sowing may have little effect on the earing of the F_1 and F_2 generations, provided the sowing time is within the normal limits, there are obvious cases where this factor is of the utmost importance. In normal early and mid-season spring varieties, there is a long period of time for sowing during which this type of variety will show normal ear emergence, and during which the difference in the time of ear emergence of the parents, although

showing some fluctuation, is never reversed by the parents' unstable behaviour. In the first four crosses in these experiments it is not probable that any great difference in the F_1 and F_2 behaviour would be apparent with sowing times within the normal period. If, however, the sowing time was abnormally late, so that the critical time of sowing for ear emergence of one of the parents was reached, then differences and abnormalities might be expected.

There are, however, cases where the time of sowing may be expected to exert a very strong effect on the earing time of the F_1 and on the type of segregation of the F_2 , even though the critical time of sowing for ear emergence of the parents is not reached. These cases occur when, owing to the unstable behaviour of one of the parents, their relative times of ear emergence may be reversed, or the difference in their times of ear emergence are much affected by the time of sowing. Examples of such cases may be seen in the two crosses involving the form *H. spontaneum* (E and F). Under the sowing and growth conditions of these observations, both F_2 progenies showed very marked transgressive segregation beyond both parents, but whereas cross E showed no obvious understandable segregation, cross F suggested a 3 : 1 ratio, the segregation of which showed little relation to the two parents.

The two crosses (Pryor's Chevallier \times *H. spontaneum* and Pryor's Chevallier \times Bocumer), which were chosen to illustrate the effect of time of sowing on the earing of hybrid progenies, do not show a reversible position in the earing time of the parents with different sowing times, but merely an increased difference in earing time with progressive lateness of sowing. In both cases, however, any differences in the hybrid progenies with sowing time are due to the later parent, because Pryor's Chevallier is extremely stable and little affected by the difference in sowing time investigated in the F_2 . In both crosses the two sowing dates showed quite distinct F_2 segregations, and it is interesting that in one sowing the Pryor's Chevallier \times *H. spontaneum* cross suggested a 3 : 1 F_2 ratio, but a single major factor difference is hardly supported by the other evidence on the earing behaviour of these two varieties, nor yet by the evidence of the second sowing of the same cross.

The great difficulty in interpreting the genetic data on the inheritance of the time of ear emergence is to find a suitable criterion for homozygosity in the F_3 , and even if such a suitable criterion is decided upon, to apply it satisfactorily. Obviously, the type of ear emergence of a pure line as represented by the parents should offer a suitable criterion, and an arbitrary mathematical calculation such as the standard error could

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be taken as the basis of comparison (Neatby, 1929). But the F_3 cultures are necessarily small populations, and many extraneous circumstances can intervene to upset the ear emergence characteristics of such populations. Observations on the day-to-day ear emergence data merely show that there are certain obviously homozygous cultures, and certain obviously heterozygous cultures, but there is a very significant proportion of cultures which is indeterminate. Some of these doubtful cultures appear to be homozygous but for some chance fluctuation which has caused an exaggerated variability. Calculation of the standard error would in such cases indicate heterozygosity, but observation strongly suggests homozygosity. It is, therefore, very doubtful whether a mathematical expression of homozygosity gives a true interpretation of the facts in the present data.

Examination of the day-to-day ear emergence of the F_3 cultures does, however, show that, even in the case of the simplest F_2 segregations, obviously homozygous and obviously heterozygous cultures occur throughout the total range of the F_2 ear emergence. There is no suggestion, for example, in the 3:1 segregation, of homozygosity of the 25% of recessives, although there is evidence that the greatest number of homozygotes occurs at the extremes of the curves, and the greatest number of heterozygotes are among the intermediate earing forms. In those crosses showing transgressive segregation, homozygous forms may be found earlier than the early parent, and later than the later parent, but in all cases, although lateness is the recessive character, the latest F_2 segregates were not necessarily homozygous.

It cannot be said, therefore, that the F_3 observations support any simple genetic difference other than the operation of one major factor in any of the crosses studied, even though the F_2 indicated a 3:1 segregation. The correlation figures between the F_2 and F_3 show that in the main the ear emergence observations on the single plants of the F_2 were accurate, while the tables of the F_3 cultures show how the increasing lateness of F_2 plants manifests itself in the F_3 . In practically all cases the F_3 plants are clustered around an earing date suggested by the F_2 plant, the range of the F_3 cultures being limited even in those most obviously heterozygous. In no case does any F_3 culture throw the extremes shown by the total F_2 , but each culture is an individualistic population, restricted in its variability, and characterized to some extent in its times of ear emergence by that of the F_2 plant from which it came. Such separate and individual F_3 populations cannot be said to be characteristic of simple genetic differences, and it seems inadequate to

try and represent any of the data of these experiments on such differences alone.

The evidence of the observations of this paper, and of the results obtained by other workers, indicates that the time of ear emergence is a character which is dependent on the reaction of subsidiary or constituent characters with the environment for its manifestation. A variety of cereal may be early under one particular set of conditions, and late under another set of conditions, while two varieties may ear simultaneously in one locality and yet possess quite different physiological characters. It therefore seems necessary to analyse or resolve the character of ear emergence time, or at any rate to study the ear emergence characteristics under different growing conditions, before the hereditary phenomena can be appreciated. In this way the true nature of "earliness" or "lateness" of particular forms can be investigated, and by identifying these characters with their physiological causes a better understanding of the genetic principles may be obtained. Phenotypic similarity with regard to time of ear emergence is no criterion of genotypic similarity, and genetic analysis must be applied, not to the arbitrary "end-product" which may be reached in various ways, but to the true underlying physiological characters of the organism.

From the somewhat superficial study of the different physiological types used in these experiments, it does seem possible to correlate physiological analysis with genetic analysis. In the first place it seems obvious that earliness may be due to the possession of different physiological characters, and that it is first necessary to analyse these. Similarity of physiological behaviour has been seen to be accompanied by lack of genetic differentiation as in the cross involving the two similar early spring types. Greater differences in physiological behaviour as expressed by increasing manifestation of the winter habit have resulted in more clear-cut genetic differences, as exemplified by crosses involving early spring forms, and mid-season forms. But in addition to absolute differences in physiological type, as interpreted by differences in time of ear emergence, the question of physiological stability in relation to the environmental conditions under which investigations are made is of great importance. Indeed, it is in connexion with this physiological instability that the most complex genetic results have been obtained in the present investigations.

The complexity of the phasic development of cereals in relation to the environmental demands has only recently been demonstrated, and it has been shown that "earliness" may be due to different physiological

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characteristics in different varieties, and particular requirements with regard to environmental stimulation are necessary for the expression of earliness. It has been suggested that excessively early types can be obtained by hybridization which combines different expressions of earliness in one plant. "Late" types are usually those which possess some degree of expression of the winter habit; Kuckuck (1933) for example says that in barley, lateness, the winter habit and winter hardiness are so closely correlated, that they cannot be regarded as distinct phenomena, while other authors use the term "winter" as synonymous with "late". Although this may in the main be true, in so far as early spring types are usually characterized by certain major requirements of temperature and light, and late winter types by other requirements of the same environmental factors, there is no doubt that varieties differ widely in their temperature and light requirements for the fullest expression of their earliness. It also appears to be true that a variety may be early and yet be a winter type, and therefore the earliness character can express itself in the absence of the spring character, although some authors deny that earliness can express itself with "winterness".

In studying the genetics of earliness and lateness it is therefore necessary to characterize varieties more accurately physiologically, and not to confuse the issues of earliness and spring type with lateness and winter type. It is only by studying varieties under different conditions of growth, or preferably under controlled conditions of temperature and light exposure, that the true nature of earliness can be assessed. Unless this is done so that the physiological basis of earliness can be understood, it is very doubtful whether any great advance can be made in the elucidation of the genetics of this very important character in cereals.

6. SUMMARY

1. The discrepancy between the results obtained by various workers concerning the inheritance of earliness or the time of ear emergence in cereals, suggests that this character needs further elucidation physiologically before genetic analysis can be properly undertaken.
2. A study of the ear emergence characteristics of varieties when grown under varying conditions indicates that the expression of this character is very much affected by the growing conditions, and the physiological basis must be understood before the various expressions of earliness and lateness are appreciated. It is therefore suggested that the genetic analysis should be conducted in conjunction with a physio-

logical analysis and with a proper consideration and understanding of the effect of environment.

3. A series of crosses involving parental forms differing in time of ear emergence, and in some cases belonging to different physiological groups, has shown how differences in genetic behaviour can to some extent be correlated with the physiology of ear emergence of the parents.

4. In one cross involving similar types, no evidence of segregation or large genetic difference was obtained. In two crosses involving larger differences of similar types, evidence for a single major factor difference was obtained. In other crosses between different physiological types, and an unstable form, more complex genetic results including transgressive inheritance were obtained. Still other crosses superficially suggested a 3 : 1 ratio in the F_2 , but the presence of a certain amount of transgression, and the behaviour of the F_3 , pointed to a more complicated relationship.

5. Two crosses involving different physiological types were studied in the F_1 and the F_2 when sown at different times in the spring by dividing the progenies into separate portions. It was shown that the behaviour of the F_1 and the F_2 of the same cross was materially affected by the sowing time.

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STUDIES IN THE NUTRITION OF VEGETABLES

PHOSPHATE DEFICIENCY AND YIELD TESTS ON SAND CULTURES OF MAY KING LETTUCE

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(With Plate II)

INTRODUCTION

ABSOLUTE lack of an essential element in the food of a plant would result in stunted growth and ultimately in death. The inclusion of increasing quantities of the element should mean more and more growth, until a point would be reached where further increases could produce no extra growth, and, in fact, might even have adverse effects.

Between this state of absolute deficiency of an essential element, and the amount necessary for optimum growth, there are obviously amounts such that though the plant lives and thrives to a certain extent, the best growth is not obtained. It is also possible, if these amounts are insufficient for the best growth, that the plant may exhibit certain symptoms (such as a definite colouring) which are characteristic of a deficiency of that element. Any such deficiency symptom is very important. Thus, in actual practice, it would be rare to have entire absence of an essential element in the soil; but it is common to have a degree of deficiency or unavailability of an element such that increased yield follows on manuring with this element; indeed, our very system of manuring is a standing proof that ordinarily there is a definite response to additions of fertilizers to the soil. It is also likely that the stage where deficiency symptoms exist is much more frequent than is generally suspected.

The present author is engaged in a study of the nutrition of vegetables, with the particular notion of ascertaining deficiency symptoms due to lack of essential elements. Field trials are nearly always valueless in this respect; for instance, the factors involved in the soil are too many and complex for one to say with any degree of certainty that a certain symptom is due to lack of a definite element. The method of procedure in this type of experiment must therefore be by the use of pot cultures in greenhouses, where factors can be controlled to some extent.

THE SAND USED FOR THE CULTURES

Sand cultures were used in this experiment.

An ideal sand for the purpose would be 100 % silica, so that it would provide an absolutely inert anchorage for the root. In practice this is impossible, but a sand can be obtained which approaches the ideal, with only minute amounts of such impurities as might vitiate the experiments. The sand finally chosen was an imported, small-grained, white sand, of approximately 99.8 % silica content. The loss on ignition was 0.15 %, and the grain size, as determined by I.M.M. sieves, was as follows:

On the	30 mesh sieve	%
	40	Nil
"	50	Nil
"	60	2.10
"	70	22.45
"	80	22.50
"	90	21.62
"	100	15.47
"	120	9.15
"	200	2.85
"	200	2.65
Through the	200	0.10
Total		98.89

The loss on screening, by difference, is 1.11 %. The apparent density of the sand is 1.60 g./c.c., the true density 2.63 g./c.c., and the pore space 39.2 % (Woodman, 1936).

The culture jars were of glazed earthenware with apertures at the bottom as in aspirators. These apertures were closed by waxed corks, through each of which ran a straight glass tube 4 in. in length ending in a short piece of rubber tubing closed by a clip on the outside of the jar. A cap of glass-wool, fixed on by pure piano-steel wire, covered the end of the glass tube inside a jar; this was found to be necessary to retain the sand, of which each culture jar contained 21 kg. (about 46 lb.).

THE CULTURE MEDIA

Eight solutions were used: A, B, C, D, E, F, G, and H. The first six, A-F, were all 0.01 % as regards each of the following: anhydrous calcium chloride, potassium sulphate, anhydrous magnesium sulphate, and sodium nitrate; anhydrous disodium phosphate and anhydrous sodium sulphate present in the media varied from 0.00 to 0.02 %. G contained phosphate alone, and H was a distilled-water control. To all the media, including the distilled-water control, pure ferrous sulphate was added in such quantity that $\frac{1}{2}$ mg. of iron (equivalent to $2\frac{1}{2}$ mg. of $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$)

was present in 1 l. of culture medium. The percentage concentrations of essential elements and of sodium present in the media are given in the following table:

Medium	pH	Percentage concentration of certain elements in the media			
		N	P	K	Ca
A	7.1	0.001648	0.004370	0.004488	0.003612
B	7.0	0.001648	0.003278	0.004488	0.003612
C	6.9	0.001648	0.002185	0.004488	0.003612
D	6.2	0.001648	0.001093	0.004488	0.003612
E	5.8	0.001648	—	0.004488	0.003612
F	5.4	0.001648	—	0.004488	0.003612
G	6.9	—	0.002185	—	—
H	6.1	—	—	—	—

Medium	pH	Percentage concentration of certain elements in the media			
		Mg	Fe	S	Na
A	7.1	0.002020	0.000050	0.004533	0.009188
B	7.0	0.002020	0.000050	0.005661	0.009188
C	6.9	0.002020	0.000050	0.006789	0.009188
D	6.2	0.002020	0.000050	0.007917	0.009188
E	5.8	0.002020	0.000050	0.009045	0.009188
F	5.4	0.002020	0.000050	0.004533	0.002706
G	6.9	—	0.000050	0.000029	0.003240
H	6.1	—	0.000050	0.000029	—

There were nine replicates of each of the treatments A–G inclusive, and three of H, a total of sixty-six cultures.

The essential elements nitrogen, phosphorus, potassium, calcium, and magnesium were contained in separate salts. This has the advantage that a detailed study of the specific effect of altering the quantity of one may be made without interfering with the other constituents of the medium, except as regards the anion (cation with nitrogen and phosphorus) linked to the essential element under experiment. Thus the phosphorus is varied in A–F, while the other essential elements remain fixed in amount.

In many respects it would be advantageous to study in one comprehensive experiment the effects of the omission, in turn, of each essential element. Seasonal effects due to factors not under control (for example, hours of daylight and sunlight, etc.) would then be common to the omission of all of the essential elements. But, if such a general study were made, it would, with a given greenhouse space and limited supplies of distilled water, apparatus, labour, etc., probably be at the expense of detail: not so many variations in concentration for each element could be used, and there would be the risk of an insufficient number of replications.

The sodium sulphate was added to B, C, D, and E, merely to keep the total quantity of sodium constant. The only variant in media A–E,

therefore, apart from the deliberate variations of the phosphate radical, was the sulphate radical attached to the sodium in the sodium sulphate; it was thought that the effect of this variation might be small, as sulphate was already present in these media to a relatively large extent. F was a medium consisting of all nutrients but the phosphate, with sodium sulphate also omitted; this was for comparison with E, to demonstrate the effect, if any, of sodium sulphate.

The salts used were, as far as possible, "AnalaR", guaranteed to be of a certain standard of purity, and to contain less than certain maxima of various impurities ("*Analar*" *Standards*, 1934). Calcium sulphate was not used, because of its small solubility, which stopped the preparation of suitable stock solutions. Calcium chloride was used instead; as the purest anhydrous salt ("*Analar*" *Standards*, 1934) contains only 70-75 % of CaCl_2 , and the purest hydrated salt, $\text{CaCl}_2 \cdot 6\text{H}_2\text{O}$, consists of "moist" crystals ("*Analar*" *Standards*, 1934), it was necessary to prepare a stock solution of calcium chloride by neutralization of a solution of pure hydrogen chloride with pure calcium carbonate.

EXPERIMENTAL

The method of experiment was as follows: the sand cultures were each given a litre of medium, keeping the clips on. This was continued daily until the sand was saturated. The clips were then removed, excess of medium thus run off, and the lettuce (cabbage lettuce, variety May King, of Watkins and Simpson) sown in the sand in the culture jars 6 February 1936.

The cultures were housed in a greenhouse maintained as nearly as possible at 50° F. They were placed on a low, central staging, and were moved round daily so as to complete the circuit of this staging once in every 3 days.

In outdoor manurial trials it is often advisable to adopt some such arrangement as the randomized block in order to allow for soil differences, etc., which might occur. With sand, particularly with a pure sample such as was used here, no variations from culture to culture are probable, and the cyclic arrangement adopted can be strongly defended. In fact the main variable in such a greenhouse experiment as this is appears to be light, and the main purpose in moving the cultures round daily was to obviate differences due to light as far as possible. The arrangement could therefore be assumed to be very similar to a randomized-block one, and the data obtained were treated on this assumption.

The clips were put on before the addition of the daily dose of medium, and taken off an hour afterwards. The quantity used daily, 500 c.c., was found to be sufficient to flood the culture, so that by this method thorough mixing of the new medium with that retained by the sand from the previous day was obtained. Later it was noticed that daily flooding for an hour tended to scorch the low-lying lettuce leaves, and this method was abandoned and the clips were kept off permanently. Even with the clips off, this amount of medium caused temporary flooding of the sand cultures and a very pronounced drip, and hence old medium must have been flushed out effectively. It is thus probable that the concentration of the media in the sand did always approximate closely to that added and desired.

Germination commenced on 12 February 1936, and was complete for every pot by the 17th. By 19 February the cultures receiving G and distilled water were noticeably darker green than the others.

On 24 February, when the cotyledons were about $\frac{1}{4}$ – $\frac{1}{3}$ in. long, and before other leaves had developed, the plants were thinned out to leave five plants per pot, one central one, and four spaced equally round this and about 3 in. from it. *A lettuce thus passed the whole of its life cycle in its particular jar, and no transplanting was necessary.*

On 12 March, the supply of medium to each culture was limited to 500 c.c. every 2 days, except when otherwise mentioned.

HYGIENE, ETC., IN THE GREENHOUSE

Successful culture work in greenhouses depends to a large extent on cleanliness, and on the prevention of insect and fungus attack.

Before the experiment, the greenhouse surfaces, stages, and culture pots were scrubbed with hot soap solution, and then swilled with water followed by a solution 2% as regards 40% formaldehyde. Weeds were pulled up from the floor of the greenhouse as they appeared. The hot pipes were painted regularly with a mixture of hydrated lime and flowers of sulphur in equal proportions made to a paste with water. The lower leaves of the lettuce were carefully lifted away from the culture sand by a blunt bone spatula an hour or so following the application of the medium.

It was, of course, undesirable to spray the lettuce. Insects were therefore controlled by fumigation with nicotine once a week, or when an attack was noticed; hand-picking was also resorted to. The nicotine fumigating solution used was home-made, and consisted of methylated

spirit containing 40 % of nicotine and 1 % of camphor, both w/v. This was used at the rate of 70 c.c. of fumigating solution, equivalent to 1 oz. of nicotine, for the greenhouse containing the cultures, which was approximately 5500 cu. ft. in volume. The dose used was thus $\frac{2}{11}$ oz. of nicotine per 1000 cu. ft. In order to get more efficient fumigation, the 70 c.c. of solution were divided into two equal lots which were then simultaneously vaporized near each end of the greenhouse.

OBSERVATIONS AND NOTES ON THE CULTURES

About this time it was noticed that cultures receiving E and F had slightly bronzed leaves (cf. Wallace (1924) for a similar symptom with apple foliage), whilst the G and H cultures continued to be darker green than the normal plants. Daily observations on the central plants were now made, and the following is a short summary of these.

Media A-D at first gave plants of normal green; E and F gave green-bronze leaves, paler with F, and bright red stalks; and G and H, dark green leaves, with radish-red or scarlet stalks. By 4 April the A-D and E and F plants were unaltered in colour; red was appearing in the G cultures, however, and the H plants were now bronzed; media E, F, G, and H, tended to give scarlet stems.

In another week E and F were tending to become purple-bronze, and G showed characteristic plants with non-crinkly broad-shaped leaves, which hugged the sand to present a flat, rosette appearance; these G cultures were coloured apple green with a dull, purple flush. The H plants were now purple, straggly plants with relatively long scarlet stalks.

By 24 April the A cultures were still normal green; of B, eight were normal green, and one had faint purple blotches; there were, with C, seven normal green, one with faint purple blotches, and one with pronounced purple patches; and with D, four normal green, two with faint purple blotches, and three with pronounced purple patches. At this time, it was possible to arrange the plants receiving treatments A-D more or less correctly according to the intensity of tinting. With E, seven were bronze, and two had died; with F, eight were bronze, and one was dead; with G, all were characteristic plants as previously mentioned; and, with H, all were purple.

May King is a tinted lettuce (reddish at the edges of the leaves from the presence of anthocyanin pigment (Brian, 1936)), especially when grown out of doors in summer. Although there seemed no doubt that

the occurrence and intensity of the purple flushes were here largely due to phosphate deficiency and not to the sunniness of this period, 500 c.c. doses of the media were given daily instead of every 2 days from 24 April in order to find out if the colour could be controlled by manipulation of the phosphate supply.

By 1 May the purple in all cultures receiving phosphate was less apparent, although this period was also sunny. The increase in the volume of medium applied and hence in the amount of phosphate supplied seemed to be responsible for this lessened intensity.

About this time a distinct difference in the "feel" of the leaves was noticed in passing from A to D. Thus lack of phosphate appeared to give a harder or tougher leaf. At first sight this could be attributed to increase in the concentration of sodium sulphate added to counter-balance the sodium phosphate withdrawn in going from A to D (as could the increase in intensity of the purple blotches, of course). But the sodium (Na^+) contents of all the media A-D were equal. It was also difficult to imagine that the increase in the sulphate radical (SO_4^{--}) accompanying the added sodium was responsible, when the minimum amount present (in A) was already relatively great because of the presence of potassium and magnesium as the sulphates. Hence the greatest probability was that this difference in texture of the leaves was due to absence of phosphate.

From 1 May, 500 c.c. of medium was given once every 3 days, in order to see if the purple colour could be intensified by lack of the total phosphate administered.

By 8 May the purple blotches had apparently been intensified by this lack of total phosphate caused by the reduction in the frequency of the dose; the consequent lack of water was not responsible, as there were no indications of an increase in purple coloration for E and F, where the same reduction in volume applied took place, though, of course, there was entire absence of phosphate as before. No deepening of the purple was noticed either with G, phosphate solution alone, even though the total amount of phosphate was reduced by curtailing the frequency of application. The H cultures were pronouncedly purple before, and could not be expected to become a deeper colour. The green lettuces were still softer than the tinted ones.

It appeared therefore that lack of phosphate, due either to a small concentration of phosphate, as with D, or to reduction in the volume of medium applied, as above, was responsible for development of the purple.

Daily applications of 500 c.c. of media were recommenced on 11 May

but, as *Botrytis* attacked two of the D cultures, the harvest had to be taken on the 15th. The following notes on the plants were made just before the harvest.

Cultures receiving A and B were normal green; all hearted and grade I. Of the C plants, one was normal in colour, hearted and grade I; the others were not grade I because of purple patches; two had very faint purple blotches, and six dull purple blotches. Four were hearted, and the other five showed definite signs of hearting up. With D, two had been removed and weighed the previous day because of *Botrytis*; of the others, one was normal green, and two had dull purple, and four pronounced purple, patches. The normal one would have been classified grade I had it hearted. One of the cultures was hearted, and the other six showed definite signs. The stalks of all lettuces treated with A-D were normal, dirty amber, in colour. With E, two were pale green bronze, two purple bronze, and five had died. The stalks were radish red. F yielded six pale green bronze plants, and one purple bronze; two were dead. The stalks were radish red. Medium G gave eight purple-bronze plants; the other was dead. The stalks were radish red and fresh looking. Medium H yielded "straggly" plants, purple and bronze in colour, with bright crimson stalks.

The tinting with A-D was markedly fainter than at the previous observation, apparently because of the renewed daily application of the media. It may be stated that, but for the colour, all lettuce plants receiving these media would have been classified as grade I on hearting.

The roots of the cultures which received A-D were bushy; those with E and F not so bushy, fewer, smaller, and not so fibrous; G gave smaller roots than E and F with fewer branches; and H tended to give tap roots merely.

Plants treated with A-D were the largest throughout the experiment. The photograph of an average plant from each series of cultures was taken on 27 April, and is reproduced (Plate II); "AQ" was the label used instead of H for the water control. The scale alongside each culture was 10 cm. in length. The photograph well indicates the effect on size of entirely omitting phosphate.

A further notion of the relative sizes of the plants may be gained from the following measurements made on 1 May; the first figure for any treatment is the average greatest spread for all the cultures, and the second the average in a direction at right angles to the first: A, 18×17 cm.; B, $17\frac{2}{3} \times 16\frac{1}{2}$ cm.; C, $16\frac{1}{2} \times 14$ cm.; D, 17×16 cm.; E, $2 \times 1\frac{1}{2}$ cm.; F, $2 \times 1\frac{1}{2}$ cm.; G, $2\frac{1}{2} \times 2$ cm.; and H, 2×1 cm.

It is at present a moot point of theoretical rather than practical interest whether lack of phosphate increases the intensity of the colour (which is then a true deficiency symptom), or whether increase in the supply of phosphate decreases the intensity of colouring, assuming the purple to be normal to May King in summer. In the preceding argument the purple blotches have been regarded as abnormal, so that the increase in intensity of colouring got by omission of phosphate has been treated as a true deficiency symptom. For all practical purposes (where a green lettuce is desirable) this is the correct method; but the distinction mentioned above still remains to be made.

HEARTING

Treatments A and B gave between them a total of eleven lettuces hearting up when treatments C and D showed none to be hearting. At the fifth harvest, lettuces undergoing treatments A and B were all eighteen of them fully hearted, while treatments C and D resulted in a total of five hearted (D was responsible for one of these only) and eleven showing definite signs of hearting. The remaining treatments gave stunted plants which would not have hearted.

There thus appears to be a limit of commercial interest in the application of phosphate to this lettuce if judged by the date of maturity. This limit lies somewhere between treatments A and B as one group, and C and D as another; and the notion is borne out and more fully discussed in connexion with yield results after the presentation of the quantitative data which follows; there also it is pointed out that growth is so rapid on approaching maturity, that earlier hearting, even by a day or so only, is of great commercial importance.

It may be mentioned here that the stunted growth and consequent lack of ability to heart characteristic of treatments E, F, G, and H, are of scientific, and not of any commercial interest.

THE YIELD, ETC., FROM DIFFERENT TREATMENTS

The tables which follow contain the quantitative and derived data obtained at the five harvests during the course of the experiment. These harvests were the first, second, third, and fourth seedling harvests, and the fifth (main, or final) harvest of the mature central cultures left after the four seedling harvests.

The seedling harvests were carried out on the four outer seedlings surrounding the central one on 8, 15, 22 and 29 April 1936, respectively.

The choice of seedling to represent each culture was made at random. The main harvest of the central plants was on 15 May 1936.

At a seedling harvest, the seedling was prised out together with a large volume of the surrounding sand so that the root was whole and undamaged. The root was then cut off at the base of the top, well washed under running tap water, dried carefully between blotting paper, and weighed. The top was also dried with blotting paper in order to remove any adherent moisture, carefully wiped and dusted free from sand with a duster, and weighed. At the final harvest, where the root was large with certain treatments, and the accompanying fibre might reach all parts of the culture jar, the head or top of the lettuce was cut off whilst the root was still in the sand, dried on the underside if necessary, cleaned, and weighed. The contents of the jar were next tipped on to a large $\frac{1}{4}$ in. mesh sieve, and the root and fibre were washed clean from sand by means of a powerful jet of water from the adjustable nozzle of a hose. The root and attached fibre were then dried as much as possible by means of dusters and, when the fibre was large in quantity, left for half an hour in the laboratory for any adherent moisture to dry off previous to the weighing.

After the tops and roots had been weighed, they were heated in water-ovens kept at 96-99° C. for 4 or 5 days or longer until their weights were constant. Thus four values were obtained for each plant: (1) the fresh weight of the top, (2) the fresh weight of the root, (3) the dry weight of the top, and (4) the dry weight of the root.

From the experimental data thus obtained for each of the cultures, the following derived statistics were calculated: (5) the fresh weight of the total plant, (6) the dry weight of the total plant, (7) the top/root ratio from the fresh weights, (8) the top/root ratio from the dry weights, and (9), (10), and (11) the percentage moisture contents of the (fresh) top, root, and total plant, respectively. A table containing summaries of the results is given and is explained in the text.

The results are calculated, as explained previously, on the assumption that the arrangement consisted of nine replicates of a randomized block for the seven treatments with solutions A, B, C, D, E, F, and G, making the total of 63 cultures. With distilled water three cultures only were set up, and the results are given later.

The actual data of the experiment were too bulky to be reproduced, though they are available on request for examination in the laboratory. The analyses of variance were worked out for the fresh and dry weights of the tops, roots, and total plants, the top/root ratios for fresh and dry

Summaries of results

Description of data	Treatment	Treatment mean	Treatment						Mean	S.E.
			A	B	C	D	E	F		
Tops, FW	I	in g.	0.063	0.037	0.028	0.028	0.031	0.029	0.017	0.006273
	SSS			A > B = C = D = E = F; B > G; C = D = E = F = G						
	II	in g.	0.150	0.154	0.050	0.081	0.031	0.027	0.017	0.01761
	SSS			A = B > C = E = F = G; A = B > D > F = G; C = D = E						
	III	in g.	0.271	0.268	0.214	0.222	0.043	0.047	0.019	0.03054
	SSS			A = B = C = D > E = F = G						
	IV	in g.	0.676	0.550	0.458	0.293	0.047	0.056	0.025	0.03657
	SSS			A = B > D; A > C = D > E = F = G; B = C						
	V	in g.	60.36	56.43	42.22	46.31	0.089	0.098	0.131	2.097
	SSS			A = B > C = D > E = F = G						
Roots, FW	I	in g.	0.011	0.012	0.009	0.016	0.029	0.029	0.014	0.002352
	SSS			E = F > A = B = C = D = G						
	II	in g.	0.043	0.052	0.010	0.014	0.021	0.020	0.012	0.03573
	NS									
	III	in g.	0.055	0.068	0.051	0.051	0.022	0.026	0.011	0.007033
	SSS			A = B = C = D > E = F = G						
	IV	in g.	0.130	0.116	0.107	0.075	0.034	0.036	0.015	0.01018
	SSS			A = B = C > D > E = F = G						
	V	in g.	18.08	17.11	11.50	12.61	0.071	0.084	0.082	0.5007
	SSS			A = B > C = D > E = F = G						
Total plants, FW	I	in g.	0.074	0.048	0.037	0.044	0.061	0.058	0.031	0.007193
	SS			A > B = C = D = G; A = E = F > G; B = E = F; E > C = G						
	II	in g.	0.194	0.206	0.060	0.094	0.052	0.047	0.030	0.02062
	SSS			A = B > C = D = E = F; C = E = F = G; D > G						
	III	in g.	0.326	0.337	0.265	0.273	0.065	0.073	0.030	0.03211
	SSS			A = B = C = D > E = F = G						
	IV	in g.	0.806	0.666	0.564	0.368	0.081	0.092	0.041	0.06437
	SSS			A > C > D > E = F = G; A = B; B = C > D						
	V	in g.	78.44	73.54	53.72	52.92	0.159	0.182	0.213	2.301
	SSS			A = B > C = D > E = F = G						

Summaries of results (cont.)

Description of data	Treatment	Treatment							Mean	S.E.
		A	B	C	D	E	F	G		
Tops, DW	I	0-009	0-004	0-005	0-006	0-009	0-009	0-009	0-007238	0-0007840
	SSS			A = E = F = G > B = C = D						
	II	0-012	0-017	0-012	0-011	0-010	0-010	0-010	0-01173	0-001521
	SS			B > A = C = D = E = F = G						
	III	0-033	0-038	0-030	0-033	0-022	0-009	0-005	0-02426	0-003547
	SSS		A = B = D > E = F = G; A = B = C = D; C > F = G; C = E							
Roots, DW	IV	0-065	0-055	0-051	0-036	0-011	0-011	0-005	0-03344	0-005793
	SSS		A = B = C > E = F = G; A = B > D; C = D > E = F = G							
	V	6-24	5-62	5-03	5-30	0-025	0-022	0-034	3-181	0-2033
	SSS		A > B = C = D > E = F = G							
	I	0-001	0-002	0-004	0-004	0-009	0-008	0-008	0-005127	0-0004533
	SSS		E = F > C = D > A = B; E > G; F = G > C = D							
Total plants, DW	II	0-004	0-008	0-002	0-007	0-010	0-010	0-008	0-007097	0-0008207
	SSS		E > B = D = G > A = B; E = F > D; B = F = G							
	III	0-015	0-019	0-015	0-020	0-010	0-008	0-005	0-01314	0-004481
	NS									
	IV	0-020	0-019	0-018	0-014	0-010	0-009	0-004	0-01329	0-001480
	SSS		A = B > D > E = F = G; A = B = C; C = D > E = F							
Top/root, FW	V	2-30	2-17	1-59	1-68	0-012	0-013	0-017	1-111	0-06123
	SSS		A = B > C = D > E = F = G							
	I	0-310	0-005	0-010	0-010	0-018	0-017	0-017	0-01237	0-0009167
	SSS		E = F = G > A = C = D > B							
	II	0-016	0-025	0-014	0-018	0-021	0-020	0-018	0-01882	0-002191
	S		B > A = C = D = G; B = E = F > C							
Top/root, FW	III	0-048	0-056	0-045	0-053	0-032	0-016	0-011	0-03738	0-004603
	SSS		A = B = C = D > F = G; A = B = D > E > F = G; C = E							
	IV	0-084	0-063	0-069	0-050	0-021	0-019	0-009	0-04673	0-006753
	SSS		A = B > D > E = F = G; A = B = C > E = F = G; C = D							
	V	8-54	7-79	6-61	6-96	0-037	0-034	0-051	4-29	0-2374
	SSS		A > B > C = D > E = F = G							
Top/root, FW	I	5-4	4-2	3-9	2-2	1-1	1-0	1-3	2-716	0-5790
	SSS		A = B = C > E = F = G; A = B > D = E = F = G; C = D							
	II	3-6	3-0	6-7	7-5	1-5	1-5	1-4	3-603	0-7677
	SSS		C = D > A = B = E = F = G							
	III	5-5	4-3	4-2	4-6	2-1	1-8	1-8	3-484	0-4003
	SSS		A = B = D > E = F = G; A > C > E = F = G; B = C = D							
Top/root, FW	IV	5-2	4-7	4-3	3-9	1-5	1-5	1-7	3-279	0-3507
	SSS		A = B = C > E = F = G; A > D; B = C = D > E = F = G							
	V	3-44	3-31	3-70	3-22	1-10	1-20	1-56	2-505	0-1994
	SSS		A = B = C = D > E = F = G							

Top/root, DW	I	ratio	7.2	2.0	1.5	1.9	0.9	1.2	1.2	2.270	0.6597
	SSS					$A > B = C = D = E = F = G$					
	II	ratio	2.8	2.7	6.2	2.9	0.9	1.2	1.3	2.473	0.3610
	SSS			$C > A = B = D > E = F$;	$A = B > G$;	$D = G$;	$E = F = G$				
	III	ratio	2.2	1.9	1.9	1.7	2.6	1.1	1.1	1.819	0.2209
	SSS			$A = B = E > F = G$;	$E > C > F = G$;	$A = B = C = D$;	$D = F = G$				
	IV	ratio	3.3	3.0	2.8	2.5	1.2	1.3	1.6	2.237	0.2839
	SSS				$A = B = C = D > E = F = G$						
	V	ratio	2.76	2.58	3.17	3.26	2.04	1.74	2.06	2.516	0.1467
	SSS			$C = D > B > E = F = G$;	$A = C = D$;	$A = B > E = F = G$					
Tops, % moisture in	I	%	85.2	90.0	76.0	75.9	72.4	65.6	46.0	73.00	2.932
	SSS			$A = B > C = D = E > G$;	$C = D > F > G$;	$E = F$					
	II	%	92.8	86.8	70.8	83.5	66.3	59.2	39.0	71.21	3.413
	SSS			$A = B = D > C = E > G$;	$C > F$;	$E = F > G$					
	III	%	87.0	84.5	85.5	84.4	46.9	81.5	71.2	77.24	3.246
	SSS			$A = B = C = D = F > G > E$							
	IV	%	90.4	89.5	88.8	87.5	73.2	80.5	78.0	83.99	1.684
	SSS			$A = B = C = D > F = G$;	$F > E$;	$E = G$					
	V	%	89.62	89.82	88.08	86.41	53.79	71.43	71.53	78.67	4.177
	SSS			$A = B = C = D > F = G > E$							
Roots, % moisture in	I	%	87.7	76.7	48.2	71.5	68.8	71.3	45.1	67.04	3.873
	SSS			$A > D = E = F > C = G$;	$A = B$;	$B = D = E = F > C = G$					
	II	%	90.3	84.9	71.1	43.4	46.7	50.6	31.5	59.79	4.087
	SSS			$A = B > C > E = F > G$;	$C > D = G$;	$D = E = F$					
	III	%	65.3	67.8	68.2	56.8	55.4	69.8	50.1	61.92	3.097
	SS			$A = B = C = F > G$;	$C = F > D = E = G$;	$A = B = C = D$					
	IV	%	84.3	83.4	82.1	80.1	70.9	76.0	75.7	78.93	1.241
	SSS			$A = B = C > F = G > E$;	$A > D$;	$B = C = D > F = G$					
	V	%	87.11	87.28	86.15	86.70	80.81	83.74	77.96	84.24	1.172
	SSS			$A = B = C = D > E = G$;	$A = C = D = F > G$;	$B > F$;	$E = F$				
Total plants, % moisture in	I	%	85.4	87.5	70.4	74.6	70.7	68.7	46.0	71.9	2.823
	SSS				$A = B > C = D = E = F > G$						
	II	%	92.2	86.7	73.0	79.3	58.8	56.2	35.6	68.81	3.833
	SSS			$A = B > C > E = F > G$;	$A > D > E = F$;	$B = D$;	$C = D$				
	III	%	83.8	81.1	82.1	79.3	50.0	77.4	63.8	73.93	1.438
	SSS			$A = B = C > G > E$;	$A > D = F > G$;	$B = C = D$;	$B = F$				
	IV	%	89.3	88.4	87.5	86.0	73.6	78.8	77.4	83.00	1.022
	SSS			$A = B = C > F = G > E$;	$A > D$;	$B = C = D > F = G$					
	V	%	89.06	89.41	87.70	86.57	70.13	78.79	75.13	82.40	1.847
	SSS			$A = B = C = D > F = G$;	$E = G$;	$F > E$					

weights, and the percentages of moisture in the tops, roots, and total plants; these analyses were made for all five harvests. The corresponding summaries of results are given in the table of that heading, together with the standard errors of the treatment means.

Key to the table containing the summaries of results

The first column is headed "Description of data". "FW" and "DW" denote respectively the fresh and dry weights of the total plant, top, or root; and the figures I, II, III, IV, and V, the first, second, third, fourth and fifth harvests. Thus the description "Tops, FW, I" refers to the fresh weights of the tops at the first (seedling) harvest; "Total plants, DW, V" indicates the dry weights of the total plant for the fifth harvest (mature plants); "Top/root, DW, IV" means the ratios of the dry weights of the tops to the corresponding dry weights of the roots at the fourth harvest; "Roots, % moisture in, III" refers to the percentages of moisture in the roots at the third harvest; etc.

In the first column there is also placed, opposite each summary of results, one of the following descriptions: "S", "SS", "SSS", or "NS". These letters indicate that the treatment results for that particular subtable are significant according to Fisher's Tables of z at the 5, 1, and 0.1 % levels, or are not significant, respectively. The value of z obtained from the data is that, $\frac{1}{2} \log_e (\text{treatments' mean square})$ minus $\frac{1}{2} \log_e (\text{error's mean square})$; it is calculated under the corresponding analysis of variance.

The second column is headed "Treatment mean", and describes how this mean is expressed (as a yield, a ratio, or a percentage, per culture, according to the subtable referred to). In the first line of the numerical data in each subtable the treatment mean, obtained by dividing the treatment total by the number of cultures per treatment, is recorded under the "Treatment" column subheadings, A to G, as the mean weight in grams, the mean ratio, or the mean percentage moisture, per culture per treatment. The mean for the whole of the results of a subtable, which is also the mean of the treatment means, is included in this first line under the "Mean" column.

Some objection may be taken on strictly mathematical grounds to the use of arithmetic means for these means and treatment means when dealing with ratios or percentages. To get any kind of a simple statistical study, however, recourse must be had to the arithmetic mean: it would be easy from the original data to obtain weighted means which took into account the size of the plant to which the ratio or percentage applied, but even then objection could similarly be made to deviations obtained

by difference. It was therefore thought better to follow the usual procedure, and to treat ratios or percentages for the plants as additive.

The last column, headed "s.e.", gives, in the first line of each subtable, the standard error of the treatment means.

The second line of each subtable is a summary of the comparisons of significance carried out on the treatment means. The signs "=" and ">" are to be read as meaning "not significantly different from" and "significantly greater than" respectively. For example, a statement, $A=B=C=D>E=F=G$, must be taken to mean that there is no significant difference between any pair of the results obtained from treatments by media A, B, C, and D, but that the four results so obtained are all significantly greater than the results obtained by using media E, F, and G, though there is again no significant difference between any pair of these three. Often more than one such statement is required to summarize the significance or otherwise of the results for a subtable.

DISCUSSION OF THE SUMMARIES OF RESULTS

As this investigation is concerned more with the effects of the various treatments on the plants (in particular at the time of the final harvest) rather than with the growth curve for lettuce for a given treatment, greater attention will be paid to differences between treatment means for different treatments at the same harvest, rather than to differences between treatment means for the same treatment at different harvests.

An inspection of the results showed that yield, whether measured for tops, roots, or total plants, was in general significantly increased at the different harvests in passing from seedling stage to final harvest within treatments which ultimately caused the lettuces to mature. The greatest increases occurred between the fourth seedling harvest and the final harvest. The top/root ratios and the percentages of moisture contained in various parts of the plants showed more complex relationships; anything of interest encountered in these relationships will be pointed out.

The treatment means in several subtables differ so greatly that it is doubtful whether the method of analysis used (one created in the first place for soil differences in field experimentation and, therefore, for much smaller differences in yield than are encountered here) is correct or not. Thus it is possible that the s.e. given in a subtable does not hold over the wide range of variation of the treatment means for that subtable. But the method of analysis followed is the standard method given for

randomized-block systems; moreover, it is not likely that any alternative method would interfere seriously with the broad conclusions which were drawn from the present analysis.

It will be gathered from the results that they were often significant at the $P=0.001$ or $P=0.01$ levels. In two cases only, Roots, FW, II, and Roots, DW, III, was non-significance due to treatments met with. The difference between the blocks' mean squares and the corresponding error's mean squares—this part of the analysis of variance is not summarized in the results given—was not usually significant; the two corresponding mean squares were more often than not of the same order of magnitude. This tends to prove that a general randomization of the cultures throughout the greenhouse would probably have been quite as effective as a randomized-block method of arrangement.

Tops, FW. At the first seedling harvest, treatment A gave the largest tops; the tops for the other treatments were not significantly different except in the single case $B > G$ (phosphate alone). At the second, B joined A as $> C$ and D, and cultures from D became relatively larger. All the phosphate cultures were greater than all the non-phosphate and phosphate-alone ones at the third harvest, which demonstrated that phosphate was of importance.

At the final harvest, $A = B > C = D > E = F = G$. The fresh weight of the tops is here of commercial importance, so that it will be of interest to note the points demonstrated by this relationship. As $A = B$, and $C = D$, there was obviously no advantage in increasing the amount of phosphate beyond that contained in B for the first two treatments, or in D for the second two: put quite simply, treatment B was as good as A, and D as C. But the increase of phosphate in passing from C and D to A and B was of special interest, as the resulting response was so great from a commercial standpoint. Thus, at the point between the two groups $A = B > C = D$ where this significant difference occurred, the increase in yield was about 40 % of the lower yields. The other significant difference of approximately 40,000 %, $C = D > E = F = G$, though relatively much greater, was of scientific and not of commercial interest; for it is unlikely that occasions would arise in practice where either no phosphate at all, or phosphate alone, would be available to the plant.

From the first harvest to the fourth, a period of 3 weeks, the increase in yield of tops for A, B, C, and D, was of the order of 900–1500 % on the lower values; from the fourth to the final harvest, about $2\frac{1}{2}$ weeks, the corresponding increases were 10,000–13,000 %. This rapid growth during the last stages is normal; because of it, even a small shortening of the

life cycle becomes important. Bearing this in mind, a truer estimate of the value of the earlier maturity caused by the treatments A and B will be obtained.

One further point is worth attention: treatments D and C gave pronounced purple blotches due to deficiency of phosphate. Yet hearting occurred with these treatments, and the yields were tolerably good. It may therefore be stated that this lettuce shows serious phosphate-deficiency symptoms, such as extreme tinting, long before the amount of phosphate is reduced to such an extent as to give negligible growth.

Roots, FW. At the first harvest the no-phosphate yields with treatments E and F were equal and both greater than all the yields from treatments which included phosphate, A, B, C, D, and G. The results were not significant at the second harvest but, at the third, all the phosphate treatments gave greater yields than the non-phosphate or phosphate alone. At the fourth harvest a differentiation of those treatments containing phosphate was apparent, for $A = B = C > D > E = F = G$; this differentiation was carried a step further at the final harvest, for then $A = B > C = D > E = F = G$, as for the tops. With treatments A and B the increase in the weights of the roots between the fourth and final harvests was about 14,000 %.

Total plants, FW. At the first harvest A gave the greatest yield; at the second, $A = B$. At the third, all the phosphate treatments were equal and gave greater yields than the non-phosphate and phosphate-alone cultures. There was still more differentiation at the fourth harvest, where $A > C > D$. At the final harvest the results agreed with those for tops and roots.

Tops, DW. It was only at the fourth harvest that the beneficial effect of phosphate on yield of dry matter for the tops became fully apparent, for then the first four treatments all gave significantly greater yields than treatments E, F, and G. At the final harvest the same arrangement obtained, except that some differentiation had then taken place between the phosphate treatments, so that treatment A gave the largest yield of dry matter of tops. There was, for treatments A, B, C, and D, an increase of about 10,000 % between the last two harvests.

Roots, DW. At the fourth harvest only did the phosphate cultures begin to show any benefit. At the final harvest the results were exactly similar to those for the fresh weights of tops, roots, or totals. The increase between the last two harvests with A and B was of the order of 11,500 %. The general trend of these results and of those for the fresh weights

favoured the notion that seedling roots were not affected by the absence of phosphate as soon as were seedling tops.

Total plants, DW. The course followed was somewhat similar to those for the dry matter of the tops and roots. At the final harvest, $A > B > C = D > E = F = G$, very similar to what might be considered in some lights the ideal arrangement, $A > B > C > D > E = F = G$, where successive increases of phosphate increase the yield successively. The increase with treatments A and B between the last two harvests was over 10,000%.

It was noteworthy that in all the dry matter results the treatments containing no phosphate and phosphate alone tended in general to give greater yields at the earlier harvests than the phosphate treatments. This might seem to indicate that the seed contained enough phosphate for the preliminary stages of dry-matter growth, especially in the tops, and that the presence of phosphate was at first deleterious to increase of dry matter; but against this the treatment with phosphate alone (G) gave results comparable with the no-phosphate treatments, E and F, and did not spoil growth in these initial stages

Top/root, FW. The phosphate treatments in general gave significantly greater ratios than the no-phosphate or phosphate-alone treatments. The presence of phosphate thus tended to increase the fresh weights of the tops of lettuce relatively more than those of the roots.

Top/root, DW. The general drift of the results was to demonstrate that this ratio was larger with phosphate. A supply of phosphate thus tended to increase the dry weights of the tops relatively more than those of the roots.

Moisture in tops, roots, and total plants. In general the percentage was increased by the presence of phosphate.

Results for distilled water

The yields of these control cultures were similar to those for the treatments with no phosphate and phosphate alone. There were three cultures only, and the following were the averages per culture at the final harvest: 0.056, 0.044, and 0.100 g., were the fresh weights of top, root, and total plant, respectively; 0.017, 0.011, and 0.028 g., were the corresponding dry weights; the ratios top/root were 1.29 and 1.44 for fresh and dry matter, respectively; and the percentages of moisture for top, root, and total plant, were 70.36, 72.86, and 71.58, respectively.

SUMMARY

Media from which phosphate was absent finally caused bronzing of the leaves of the resulting stunted plants of May King lettuce grown in sand culture, and red or crimson stalks. Phosphate alone produced characteristic purple (and/or bronze) and apple-green, flat, stunted rosettes with broad, non-crinkly leaves, and red stalks. Water alone caused stunted, straggly, purple plants, with relatively long, crimson stalks.

Where some phosphate was supplied in addition to the other essential elements, a plant of normal colour resulted at first. Later, purple blotches appeared on the plants receiving inadequate supplies; the intensity of this purple became greater as the amount of phosphate in the medium diminished, and it could be controlled by varying the concentration of phosphate in the medium or the frequency of application. Another deficiency symptom was the tougher leaf resulting from a lack of phosphate. A sufficiency of phosphate caused earlier maturity.

The media which contained the two greatest concentrations of phosphate were the best of those used because they gave the best growth, lettuces of the best colour without purple blotches, earlier maturity, and tenderer leaves.

The final yields of heads were statistically the same with the two heaviest phosphate treatments, and both were greater by about 40 % of the lesser yields than the two statistically equal yields with the lower amounts of phosphate. All the phosphate treatments gave yields superior by about 40,000–60,000 % to the non-phosphate and phosphate-alone yields, but this second difference had no commercial significance. Similar results were obtained for the roots, and for the dry weights of the tops and roots.

Increasing the phosphate supply increased the fresh and dry weights of the tops relatively more than those of the roots. In general, the percentages of moisture in both tops and roots were also increased by a greater supply of phosphate.

Results are also given for the lettuce at four seedling stages.

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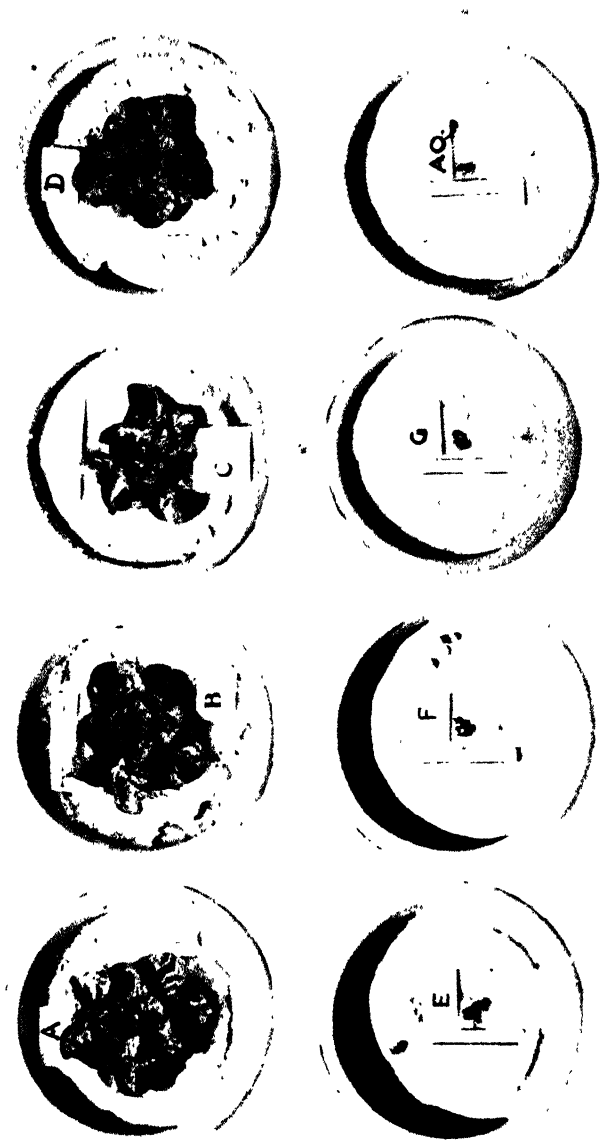
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(Received 30 May 1938)



A representative plant of each series of cultures photographed 27 April 1936.

ANALYTICAL YIELD INVESTIGATIONS ON NEW ZEALAND WHEAT

IV. BLENDING VARIETIES OF WHEAT

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(With Two Text-figures)

INTRODUCTION

To meet the changes in environment imposed upon plant growth by the unavoidable variation of weather, soil and management, the plant breeder has the choice among four alternatives. He may aim at producing a variety of great adaptability, an all-round variety, to suit the requirements of a larger district. He may produce varieties suitable for more narrowly confined conditions, thus aiming at a higher degree of specialization. He may advocate the cultivation of a number of more or less similar varieties which would tend to level out the uncertainties resulting from seasonal fluctuations in the return of any one variety. Or, lastly, he may advocate the sowing of such varieties in a blend. The blending of varieties in one crop, apart from its possible value as a yield stabilizer, may conceivably raise the composite yield of the blend beyond the mean of its components' yields when grown separately. The differences in physiological requirements and growth rhythm of the component varieties may create better conditions for the individual plant in a blend than in a pure population, where the requirements of all members are closely similar as well as simultaneous.

The use of mixed cultures embracing different species is as old as farming itself. The unconscious cultivation of varietal mixtures of one species is equally ancient. When in the course of the nineteenth century pure-bred varieties replaced mixed crops, rational blending of individual lines became possible. According to Nuding (1936), v. Rümker (1892) was the first author to advocate the use of varietal blends. Engelke (1935a) and Nuding (1936) have reviewed the older literature.

Accurate experiments, designed to test the productivity of blends, are confined to recent years. Engelke (1935a) blended two varieties of wheat in varying proportions. The yields of all blends were higher than those calculated from the yields of the pure varieties, and in some instances higher than that of the high-yielding component. "Crop

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density", i.e. the number of heads per unit area, was also higher in the blends, but the weight of 1000 grains was not improved.

Nuding (1936) reported on blending trials comprising four varieties of wheat which were tested in 50 : 50 blends, in all their combinations, against the pure varieties. The experiments were conducted for three years, in seven localities of widely different character. The varieties included exhibited large developmental and morphological differences. The results showed a characteristic tendency for blends to exceed the mean yields of their components, which was especially marked in the blends of those varieties which were suitable for any particular district. It is claimed that blending of suitable varieties reduces the risk of crop failure, especially under unfavourable circumstances. The "crop density" of blends as a rule approximated to the mean of the components. The number of grains per ear and the weight of 1000 grains had a tendency to fall slightly below the means. The blends were treated *in toto*, the yield characters being determined on the mixed population, but not on the components. The grain produced in the blends was used for sowing the same blend in the succeeding season; consequently, changes in the composition of the blends could be followed from year to year. These were very marked where one of the components was more suitable or adaptable than the other. Similar changes in the proportions of the blends were reported by Klages (1936). In a mixture of durum and hard red winter wheats, the durum components showed a marked increase, owing to abnormal climatic conditions.

Harlan & Martini (1938) described the effect of natural selection on a mixture of eleven varieties of barley grown at ten stations for periods ranging from 4 to 12 years, seed being saved for the following year. The less adaptive components were quickly eliminated.

Heuser (1938) concludes from 3 years' blending trials of five wheat varieties, all eminently suitable for the local conditions, that the pure varieties yield at least as well as the blends. There is even a tendency for lower yields in the latter.

In the study reported below, in the first instance an attempt was made to find high-quality lines which, when blended with the standard variety, Tuscan, would return a composite yield at least as high as that of the standard. In those trials which included a line yielding less than Tuscan, only a yield surpassing the mean of the components' yield would be satisfactory. The lines included in these trials were closely similar to Tuscan in morphological characters, in development and in yield. This similarity of the components appeared to be a primary condition of

success, both in view of the climatic conditions, which would not favour wide differences of development, and of the established principles of wheat growers and flour millers.

The main part of this investigation was directed towards an analytical study of the components of varietal blends. For this purpose plants of pure varieties and of the same varieties grown in blends of varying proportions were submitted to an analysis of their yield characters, viz. yield per plant (*p*), number of heads per plant (*e*), yield per ear (*h*), number of grains per ear (*n*) and weight of 1000 grains (*g*). From these results conclusions could be drawn on the mutual effect of blended varieties on yields and yield components.

The following are the lines which were used in blending trials:

Line	No.	Parents
A	$F_7: 31.03$	Tuscan \times White Fife
B	$F_7: 31.05$	
C	$F_8: 60$	
D	$F_8: 60.23$	
E	$F_8: 60$	(Tuscan \times Marquis) \times Tuscan
F	$F_8: 60$	
G	$F_8: 60.52$	
H	$F_8: 60.24$	
J	$F_8: 60.28$	(Tuscan \times Reward) \times Tuscan
K	$F_8: 60.46$	
L	$F_8: 64.25 (64.02)$	

A. FIELD TRIAL, 1935-6

This trial included Tuscan, two breeding lines, and blends of 75% of Tuscan with 25% of each of these lines. The trial was sown with a drill, in plots of 2.2 chains \times 1 yard, with ten replications. The rate of seeding was 2 bushels per acre. The mean yield of Tuscan was 66.6 bushels per acre. The three varieties are closely similar in general appearance. They all headed and ripened within 1 or 2 days.

Table I illustrates the observed yields—in percentage of that of Tuscan—together with the corresponding proportions of the pure varieties ("calculated yields"). Whilst in the blend of A observed and

Table 1. *Field trial*, 1935-6

Variety or blend	Yield (% of Tuscan)	
	Observed	Calculated
Tuscan	100	—
A. (31.03)	115.9	—
75% Tuscan + 25% A	104.2	104.2
B. (31.05)	121.0	—
75% Tuscan + 25% B	107.4	103.7

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calculated yields are identical, that of B yielded 3·7% above the expectation, an increase which presumably is devoid of significance.

B. SMALL-SCALE YIELD TRIALS, 1935-6 AND 1936-7

This series included nine separate trials, eight being conducted in 1935-6 and one in 1936-7. Each of them comprised five treatments: Tuscan, one breeding line, and three blends of the two varieties, with 10, 20 and 30% of the line respectively; except that in the ninth trial, the blends contained 10, 25 and 50% of the line. Each plot consisted of one single row of 16 ft. length, sown by hand at the rate of 10 g. per plot. The rows were 1 ft. apart. There were ten replications (randomized blocks). All breeding lines were similar to Tuscan in type and in development.

Table II. *Small-scale yield trials, 1935-6 and 1936-7*

		Yields in percentage of Tuscan					
			90 % Tuscan	80 % Tuscan	70 % Tuscan		
Line		Tuscan (1)	10 % Line (2)	20 % Line (3)	30 % Line (4)	Line (5)	Statistically significant differences
C	Observed	100	98·8	97·8	97·4	90·0	(1) and (2) > (5)
	Calculated		98·9	97·9	96·9		
D	Observed	100	103·2	104·9	103·7	97·1	—
	Calculated		99·7	99·4	99·1		
E	Observed	100	107·3	102·0	102·1	96·4	—
	Calculated		99·6	99·2	98·9		
F	Observed	100	96·4	97·3	93·3	78·7	(1), (2), (3) and (4) > (5)
	Calculated		97·9	95·5	93·6		
G	Observed	100	101·8	97·5	96·7	91·4	—
	Calculated		99·1	98·3	97·4		
H	Observed	100	100·0	98·7	97·9	102·3	—
	Calculated		100·1	100·4	100·6		
J	Observed	100	97·4	96·4	95·8	85·9	(1), (2), (3) and (4) > (5)
	Calculated		98·4	97·1	95·7		
K	Observed	100	103·5	100·1	98·4	103·7	—
	Calculated		100·3	100·6	101·1		
			90 % Tuscan	75 % Tuscan	50 % Tuscan		
			10 % Line	25 % Line	50 % Line		
L	Observed	100	103·4	102·0	99·0	105·0	—
	Calculated		100·5	101·0	102·5		

The results, in proportion of the yields of Tuscan, are shown in Table II and in Fig. 1. The following conclusions can be drawn:

(1) In the majority of the lines, viz. C, F, G, H, J, K and L, the observed yields of the blends are in close proximity to those calculated from the yields of the pure varieties.

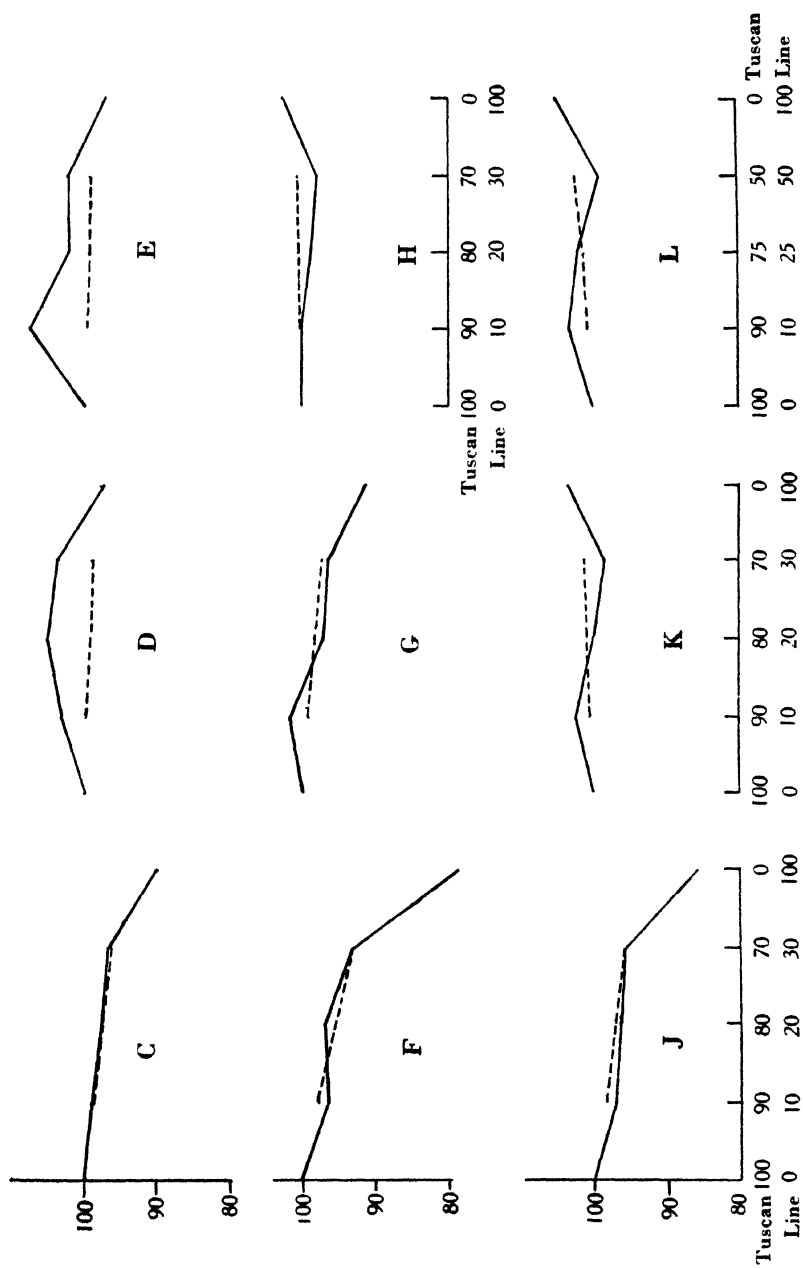


Fig. 1. Small-scale blending trials. Tuscan blended with lines C-L; observed —, calculated - - - -.

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(2) In no one of the trials is any blend significantly below expectation.

(3) In the lines D and E, all blends yield above expectation. None of these increased yields, however, is statistically significant.

It can therefore be concluded that in all nine trials the yields of the blends are very closely similar to the expectation calculated from the yields of the component varieties. Only in two out of the nine varieties is there any indication of an increased yield due to blending.

C. ANALYTICAL TRIALS, 1935-6 AND 1936-7

With the object of applying the yield analytical methods to the problem of the blending of varieties, three experiments were conducted, containing Tuscan in blends with the breeding lines D, G and L, all of which were also tested in small-scale yield trials (see the previous section). It was intended to estimate the modification in the yield structure of plants grown in a mixture of two varieties, in comparison with that of the same varieties grown in pure sowings.

Each trial consisted of five treatments:

- (1) Pure Tuscan.
- (2) Pure line (D, G or L).
- (3) 90 % Tuscan + 10 % Line.
- (4) 75 % Tuscan + 25 % Line.
- (5) 50 % Tuscan + 50 % Line.

The plots were sown with the Woodfield dibbler, giving an equal spacing of 8×2 in. The seeds of the "line" were evenly spaced among the Tuscan plants (e.g. in treatment 2 every tenth seed in the row) and, at the time of sowing, they were marked with a painted wire, permitting their identification at harvest. Each plot consisted of 160 plants, with the exception of treatment 3, which, to give a sufficient number of "line" plants, contained 240 plants. Each plot had a border sown in the same manner as the plot itself, which was removed at harvest. There were two replications in 1935-6 (lines D and G) and three in 1936-7 (line L). In this latter trial, an error in harvesting necessitated the deletion of treatment 4. In the blends, Tuscan and "line" plants were harvested separately. The yields per row of forty plants were estimated from the average yield per plant; in the blends the average yields per plant of Tuscan and of the "line", in the given proportions, were used. The "calculated" values for yield per row were obtained by computing the appropriate proportions of the Tuscan and "line" values from treatments 1 and 2.

The yield characteristics determined, together with the abbreviations used, were as follows:

- r* yield per row (grams),
- p* yield per plant (grams),
- e* number of ears per plant,
- h* yield per ear,
- n* number of grains per ear,
- g* weight of 1000 grains (grams).

The results are recorded in Tables III and IV and in Fig. 2.

(a) Yield per row

The lines used in these trials were D, G and L. D in previous trials had yielded significantly less than Tuscan, G and L approximately the same as Tuscan. In the small-scale blending trials recorded above (Table II), there are no significant differences between any of these three lines and Tuscan.

The yield per row of D and G in their pure sowings is in accordance with these experiences. D yields somewhat less than Tuscan, G about the same as the standard. Line L, however, yields appreciably more. This, it is suggested, is due to an exceptionally low yield of the pure Tuscan plots. For not only is the high yield of L contrary to all experience with this line in the same, in previous and in later seasons, but the difference between the yield of Tuscan sown pure and sown in the 10% blend, seems far too large to be mainly due to blending.

The yields per row of the blends are above the expectation (Fig. 2), with the exception of L, where, presumably owing to the low yield of pure Tuscan, the first blend (90% Tuscan) yielded well above expectation.

(b) Yield analysis of line D and its blends

The yield per plant of this line is strikingly depressed by blending with Tuscan. All yield components are affected, but least of all *g*. There is a slight recovery in the 50% blend in comparison with the 10 and 25% blends. The Tuscan yield and yield components are markedly superior in the blends as compared with the pure sowings, yet it is more the general tendency than the individual increases which can be considered as significant. It cannot, for example, be thought likely that an admixture of 10% of the line would appreciably raise the yielding capacity of the 90% of the population which consists of Tuscan plants. Yet there appears to be a general tendency for greater productiveness which is apparent in all yield characters. Were it not for the increased

Table III. *Analytical trials, 1935-6 and 1936-7*

Treatment	(a) Line D						Line D			r			
	Tuscan						p	e	h	n	g	Observed	Calculated
(1) Tuscan	3.56	4.19	0.85	19.20	44.2	—	3.20	3.58	0.90	22.49	39.7	142.0	—
(2) D	—	—	—	—	—	—	3.20	3.58	0.90	22.49	39.7	128.0	—
(3) 90% T + 10% D	3.74	4.22	0.89	19.36	45.7	—	2.13	2.88	0.74	20.34	36.4	143.1	141.0
(4) 75% T + 25% D	3.97	4.34	0.91	19.83	45.9	—	2.13	2.81	0.76	19.87	36.3	140.2	138.8
(5) 50% T + 50% D	4.13	4.58	0.90	19.83	45.2	—	2.45	3.13	0.78	20.34	38.1	131.6	135.2

Treatment	(b) Line G						Line G			r			
	Tuscan						p	e	h	n	g	Observed	Calculated
(1) Tuscan	3.32	4.35	0.77	17.86	42.7	—	3.45	3.85	0.90	21.45	41.9	132.8	—
(2) G	—	—	—	—	—	—	3.45	3.85	0.90	21.45	41.9	138.0	—
(3) 90% T + 10% G	3.36	4.15	0.81	18.47	43.8	—	2.73	3.57	0.76	19.15	39.5	131.9	133.3
(4) 75% T + 25% G	3.29	4.24	0.78	17.81	43.7	—	2.64	3.64	0.73	18.71	38.8	125.1	134.1
(5) 50% T + 50% G	3.68	4.39	0.84	18.80	44.6	—	2.70	3.56	0.76	19.11	39.8	127.6	135.4

Treatment	(c) Line L						Line L			r			
	Tuscan						p	e	h	n	g	Observed	Calculated
(1) Tuscan	3.10	3.05	1.02	23.07	44.2	—	3.57	3.54	1.00	21.67	46.2	124.0	—
(2) L	—	—	—	—	—	—	3.57	3.54	1.00	21.67	46.2	142.8	—
(3) 90% T + 10% L	3.62	3.25	1.12	23.76	44.8	—	3.53	3.16	1.12	24.00	46.6	144.4	125.9
(5) 50% T + 50% L	3.64	3.53	1.03	22.75	45.2	—	3.23	3.23	1.00	21.38	47.0	137.4	133.4

Table IV. *Analytical trials, 1935-6 and 1936-7*

Yield characteristics in % of Tuscan (treatment 1)												
(a) Line D												
Treatment	Tuscan				Line D				r			
	p	e	h	n	g	p	e	h	n	g	Observed	Calculated
(1) Tuscan	100	100	100	100	100	—	—	—	—	—	100	—
(2) D	—	—	—	—	—	89.8	85.4	105.8	117.1	89.8	89.8	—
(3) 90% T + 10% D	105.0	100.7	104.7	100.8	103.3	59.8	68.7	87.0	105.9	82.3	100.4	99.0
(4) 75% T + 25% D	111.5	103.5	107.0	103.2	103.8	59.8	67.0	89.4	103.4	82.1	98.4	97.4
(5) 50% T + 50% D	116.0	109.3	105.8	103.2	102.2	68.8	74.7	91.7	105.9	86.1	92.4	94.9
(b) Line G												
Treatment	Tuscan				Line G				r			
	p	e	h	n	g	p	e	h	n	g	Observed	Calculated
(1) Tuscan	100	100	100	100	100	—	—	—	—	—	100	—
(2) G	—	—	—	—	—	103.9	88.5	116.8	120.1	98.1	103.9	—
(3) 90% T + 10% G	101.2	95.4	105.1	103.4	102.5	82.2	82.0	98.7	107.2	92.5	98.9	100.3
(4) 75% T + 25% G	99.0	97.4	101.2	99.7	102.3	79.5	83.6	94.8	104.7	90.8	94.2	100.9
(5) 50% T + 50% G	110.8	100.9	109.0	105.2	104.4	81.0	81.8	98.7	107.0	93.2	96.0	101.9
(c) Line L												
Treatment	Tuscan				Line L				r			
	p	e	h	n	g	p	e	h	n	g	Observed	Calculated
(1) Tuscan	100	100	100	100	100	—	—	—	—	—	100	—
(2) L	—	—	—	—	—	115.1	116.0	98.0	93.9	—	115.2	—
(3) 90% T + 10% L	116.7	106.5	109.7	102.9	101.3	113.8	103.6	109.7	104.0	105.4	116.5	101.5
(5) 50% T + 50% L	117.4	115.7	100.9	98.6	102.2	104.1	105.9	98.0	92.6	106.3	110.8	107.6

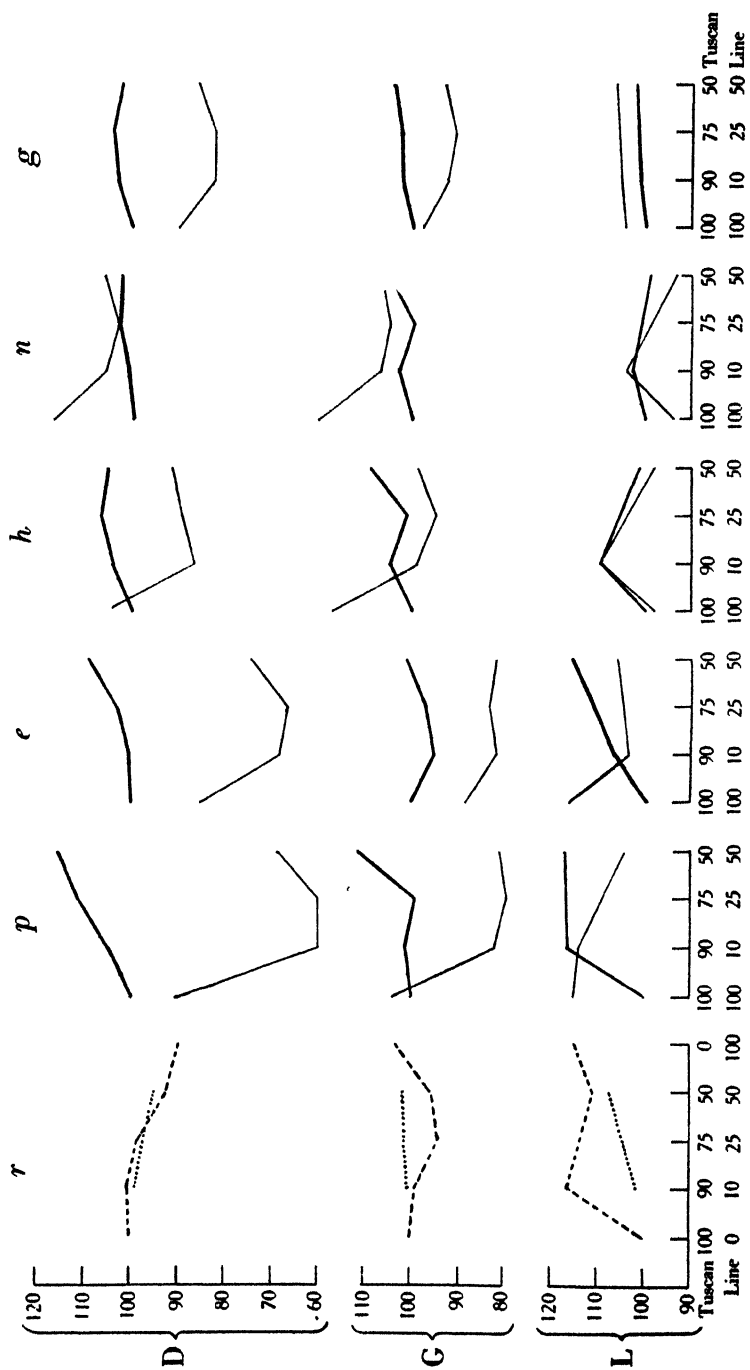


Fig. 2. Yield per plot (r) and yield characters (p, e, h, n, g) in pure and blended populations of Tuscan and lines D, G and L.
 r : observed, calculated; p, e, h, n, g : ——— Tuscan, ——— line.

production from the Tuscan plants, the yield per row (r), owing to the yield depression of the plants of line D, would be markedly below the expectation calculated from the pure sowings.

(c) *Yield analysis of line G and its blends*

In the blends, line G also shows a marked loss in its yield per plant, as compared with the pure sowing. Yet the yield decrease is considerably smaller than in line D. Whilst in the latter both e and h were about equally affected, e of line G is nearly constant, but h is depressed in the blend. This is chiefly due to the detrimental effect of blending on the number of grains per ear (n).

Tuscan also is modified to a smaller degree than is the case in blending with line D. The only marked variation from the pure sowing occurs in the 50% blend, where the increased yield per plant is mainly due to the larger number of grains per ear. The slight depression of the line, only to a small degree balanced by an improvement of Tuscan, results in the yields per row for the 25% and the 50% blends being somewhat below the expectations.

(d) *Yield analysis of line L and its blends*

There is a minor depression in the yield per plant of the line in the 50% blend. e is somewhat lowered in both blends, which, however, is balanced in the 10% blend by an increased h . The latter is due to the high n of the line in this blend—more likely than not due to environmental circumstances.

The low yield of Tuscan in its pure sowings has been discussed above. The only marked influence of blending on the development of Tuscan is a tendency to higher ear production (e) in the blends.

(e) *Conclusions*

(1) In small-scale yield trials (see the previous section), as well as in the trials reviewed in this section, the three lines included yielded in pure sowings about the same as Tuscan. In blends with the latter variety they approximated to the expectation calculated from pure sowings. Yet the yield structures of the line, as well as that of the Tuscan plants with which it was interspaced, were modified in a different manner in each of the three cases.

Line	Yield characters mainly modified					
	Line			Tuscan		
D	e	n	(g)	e	(n)	(g)
G	(e)	n	(g)		n	
L	e			e		

(2) In none of the three experiments was Tuscan depressed by blending either in its yield per plant or in any of its yield components. Since at least two of the lines generally yield the same as Tuscan, these studies illustrate the aggressiveness of this variety in competition.

(3) The results of these analytical studies demonstrate the complexity of the interrelations of varieties when grown in mixed populations. Varieties may depress others and themselves compensate or over-compensate for such losses. Yet there is apparently a wide range of variation in mutual reactions. Any predictions on the agronomic value of varietal blends would have to take cognizance of these complexities, which doubtless are subject to a further source of variation due to changes in environmental conditions.

D. THE BAKING QUALITY OF INTERVARIETAL BLENDS

(1) *Field trial*

In baking tests, Tuscan, lines A and B, their "grown" blends, and blends composed of proportionate parts of these varieties from their pure sowings ("artificial blends") were closely similar. The "grown" blends, however, though similar in strength to the artificial blends, required a distinctly longer fermentation period. Farinograms of the pure sowings, "artificial" and "grown" blends were almost indistinguishable; results of fermentation tests after Pelschenke for all treatments were within 6 min. (45-51).

(2) *Small-scale yield trials*

In baking tests, the nine lines ranged between medium and strong. Tuscan, itself a medium wheat, was weaker than all but one line (G), with which it was equal. In the strongest line, the blends improved in proportion to the quantity of the line. The weaker lines caused no noticeable improvements. Six of the nine lines were also submitted to "artificial" blending (from pure sowings). These blends were similar to the "grown" blends in baking behaviour. One "artificial" blend required markedly less fermentation than the corresponding "grown" blend; in another this relation was reversed.

Engelke (1935 *a, b*), testing blends by his Göttinger method, found in some instances improvements through blending which exceeded the means of the pure varieties. Similar results are frequently obtained in blending wheats grown separately. There is no evidence that "grown" blends differ in quality from blends obtained by mixing the same lines grown separately under identical conditions.

SUMMARY

1. An endeavour was made to obtain a blend of Tuscan wheat with a high quality line which would yield as much as Tuscan, at the same time possessing a superior baking quality. Of the eleven lines which were blended with Tuscan, nine blends returned yields corresponding to the expectation calculated from the pure varieties, and two blends yielded more than the expectation; these increases were not statistically significant.

2. Tuscan, three lines and their blends were submitted to yield analytical treatment. The yield characters of the components of blends were compared with their yield characters when grown by themselves. Whilst the yields per plot of the blends corresponded to the expectation, the yield analyses revealed that the component varieties exerted a modifying influence on each other, which was different in each of the three trials. Tuscan demonstrated its aggressiveness by depressing in every case the yield characters of the lines with which it was blended.

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PERMEABILITY OF SATURATED SANDS, SOILS AND CLAYS

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It has long been known that, in any porous medium, the rate of flow of a fluid through the medium is proportional to the pressure gradient in the direction of flow (Muskat, 1937). Thus, if Q c.c./sec. are obtained from a column of length L cm., and cross-sectional area A cm.², when the pressure difference across the column is ΔP g./cm.², then

$$u = \frac{Q}{A} = K \frac{\Delta P}{L} \quad (\text{D'Arcy's law}), \quad \text{.....(1)}$$

where u is the apparent linear rate of flow in cm./sec., and K is a coefficient. It is also generally recognized (Muskat, 1937) that u is inversely proportional to the viscosity of the fluid, η poises, whence

$$u = K_1 \frac{\Delta P}{\eta L}. \quad \text{.....(2)}$$

Then K_1 , which will be called the permeability, depends only on the nature of the bed, and is independent of the fluid, of the pressure gradient, and of the dimensions of the bed. In short, in a bed of rigid particles, the permeability depends only upon the size, shape, and mode of packing of the particles forming the bed. Many attempts have been made to calculate K_1 theoretically from these variables. The most widely known and accepted is that of Slichter (1897-8), whose equation for a bed of uniform spherical particles of diameter d cm. can be put in the form,

$$K_1 = 10 \cdot 2 \frac{d^2}{K_2}, \quad \text{.....(3)}$$

where K_2 is a function of the porosity ϵ , and varies from 84.3 when $\epsilon = 0.26$ to 12.8 when $\epsilon = 0.46$, these being approximately the extreme limits of ϵ for spheres in regular modes of stacking. The variation in K_2 stresses the importance of changes in porosity, and is, indeed, in rough agreement with experimental values. In recent years, the theoretical basis of Slichter's equation has been attacked (Graton & Fraser, 1935; Darapsky, 1912), and, further, it has always suffered from the incon-

venience that no guidance is given for an "effective diameter" to be substituted for d when particles are neither uniform nor spherical.

In the newer type of treatment (Kozeny, 1927; Carman, 1937, 1938; Krüger, 1918), size and shape of particle are included by the specific surface, S_0 cm.²/cm.³ For uniform spheres, $S_0=6/d$, and, conversely, for irregularity of size and shape, one can define, if desired, an effective diameter $d_m=6/S_0$. In Kozeny's equation (Kozeny, 1927; Carman, 1937),

$$K_1 = \frac{g}{k S_0^2} \frac{\epsilon^3}{(1-\epsilon)^2}, \quad \text{.....(4)}$$

or, since $g=980$ cm./sec.², and k is found experimentally to be 5.0,

$$K_1 = \frac{196}{S_0^2} \frac{\epsilon^3}{(1-\epsilon)^2}, \quad \text{.....(4a)}$$

where the effect of porosity is given by the porosity function, $\epsilon^3/(1-\epsilon)^2$. The derivation of this equation is as follows.

In a circular pipe, Poiseuille's law is given by

$$u = \frac{g d_e^2}{32} \frac{\Delta P}{\eta L}. \quad \text{.....(5)}$$

Now, if, instead of the diameter d_e , one uses the hydraulic radius m , where

$$m = \frac{\text{volume of pipe}}{\text{area of wetted surface}}, \quad \text{.....(6)}$$

it is seen that
$$m = \frac{\pi}{4} d_e^2 L \div \pi d_e L = \frac{d_e}{4}, \quad \text{.....(7)}$$

so that
$$u = \frac{g m^2}{2} \frac{\Delta P}{\eta L}. \quad \text{.....(8)}$$

In this form the equation becomes roughly applicable to pipes which are not circular in section. Thus, for rectangular and elliptical pipes, if one were to replace k_0 for the factor 2.0, k_0 would vary as follows:

Shape of cross-section	k_0
Circle	2.0
Ellipse:	
(a) major axis = 2 × minor axis	2.13
(b) major axis = 10 × minor axis	2.45
Rectangles:	
(a) width = height, i.e. square	1.78
(b) width = 2 × height	1.94
(c) width = 10 × height	2.65
(d) width is infinite	3.00

More complex shapes fall within the same limits of k_0 , the majority grouping in the region $k_0=2.0-2.5$. Now, the pore space in a granular

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bed may be regarded as a single channel of rather involved shape, but of constant cross-sectional area, namely, ϵA , where ϵ is the porosity and A is the total area of the cross-section. If the cross-sections of the pore-space were divided arbitrarily into simpler shapes, there would be a preponderance of elongated shapes, comparable with rectangles and ellipses, rather than circular, square and triangular shapes. Thus, if equation (8) were to be applicable, one would expect k_0 to be nearer 2.5 than to 2.0. It is particularly to be noted that the assumption of a constant fractional free area within a given bed implies a random packing of the particles. In regular modes of packing, as Graton & Fraser (1935) have remarked, there is a large and regular variation of fractional free area from cross-section to cross-section; and the average fractional free area in one direction is different from that in another, so that permeability would vary with the orientation of flow to the structure of the bed. A completely random arrangement, from its very nature, must have the same permeability in all directions, and this is also in accord with experimental observations.

The essential part of the Kozeny theory lies in applying equation (8) to granular beds. Once one has assumed that this is feasible, further refinements are readily introduced. First, correction has to be made for the actual length, L_e , of the path taken by the fluid as it passes through a bed of thickness L . Second, the actual velocity of the fluid in the pore-space will not be u , i.e. the apparent velocity over the total area, A , since the free cross-sectional area is only ϵA , and, further, it must actually travel a distance L_e when appearing to travel a distance L . Thus, the actual velocity will be $\frac{u L_e}{\epsilon L}$. Summarizing these points, one obtains

$$\frac{u L_e}{\epsilon L} = \frac{m^2}{2.5} \frac{\Delta P_g}{\eta L_e} \quad \text{.....(9)}$$

$$\text{or} \quad u = \frac{\epsilon m^2}{2.5} \frac{\Delta P_g}{\eta L} \left(\frac{L_e}{L} \right)^2, \quad \text{.....(10)}$$

$$\text{and, if one substitutes} \quad u = K_1 \frac{\Delta P}{\eta L},$$

$$\text{then} \quad K_1 = \frac{\epsilon m^2 g}{k}, \quad \text{.....(11)}$$

$$\text{where} \quad k = 2.5 \left(\frac{L_e}{L} \right)^2. \quad \text{.....(12)}$$

Evaluation of m is readily made, since it is merely the ratio of the

pore-space per unit volume of the bed, ϵ , to the surface per unit volume of the bed, S ,

$$\text{i.e.} \quad m = \frac{\epsilon}{S} \quad \text{.....(13)}$$

$$\text{and} \quad K_1 = \frac{g}{k} \frac{\epsilon^3}{S^2} \quad \text{.....(14)}$$

Since particle volume per unit volume of the bed is $(1 - \epsilon)$,

$$S = (1 - \epsilon) S_0, \quad \text{.....(15)}$$

$$\text{whence} \quad K_1 = \frac{g}{k S_0^2} \frac{\epsilon^3}{(1 - \epsilon)^2} \quad \text{.....(4)}$$

Experiments by the writer (Carman, 1937) have indicated that, on the average, a fluid flows at 45° to the axis of the bed, i.e., to the direction in which flow is measured. This would make $L_e/L = \sqrt{2}$, so that the theoretical value of k is 5.0, in agreement with the value obtained by experiment.

EXPERIMENTAL EVIDENCE FOR KOZENY'S EQUATION

A great deal of evidence for equation (4) has been collected and discussed elsewhere (Carman, 1937), and the writer has also investigated the equation systematically for variations of viscosity, of particle size, of particle shape, and for mixtures of particles of various sizes and shapes (Carman, 1938). These tests cover a range of porosity from 0.26 to 0.9, which corresponds to a 2000-fold range of the porosity function, $\epsilon^3/(1 - \epsilon)^2$, the most characteristic feature of Kozeny's equation. A notable point in these investigations has been the constancy of k under all conditions. Theoretically, variations of the order of 20 % might well have occurred, since both k_0 and L_e/L might be expected to vary with the shape of the pore-space. The actual variation in k is within 5 %, so that, for a given specific surface and porosity, the permeability is fixed within this limit of accuracy. The writer has made use of this fact for the converse process of determining specific surface from permeability measurements.

In the experiments just cited, the least particle size was $d_m = 89 \mu$. In a second part, to be published shortly, verification of Kozeny's equation has been extended to particles with an effective diameter, $d_m = 2.7 \mu$. It is sufficient here merely to present a few data to illustrate the method of approach and the agreement obtained.

In order to obtain an absolute test of Kozeny's equation in the range $d_m = 10 \mu - 100 \mu$, a powder of spherical glass particles, prepared by the

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method of Sklarew (1934), was divided into three fractions of three different sizes, and each examined microscopically. The size analyses, each based on a count of 1000 particles, are shown in Table I. The total area of 1000 particles is $\pi \Sigma N d^2$, and the total volume, $\frac{1}{6} \pi \Sigma N d^3$, so that the specific surface, S_0 , is given by $S_0 = \frac{6 \Sigma N d^2}{\Sigma N d^3}$, and the average particle size, d_m , by $d_m = \frac{\Sigma N d^3}{\Sigma N d^2}$. These data were then used to obtain the calculated values of K_1 in Table II, where they are compared with "observed" permeabilities. It will be noted that agreement was equally good using both absolute ethyl alcohol and acetone, showing the validity of equation (4).

Table I. *Size analyses of spherical glass particles*

Size range in μ	Average size in range d μ	Number of particles, N		
		Fraction I	Fraction II	Fraction III
2-5	3.5	38	—	—
5-10	7.5	109	—	—
10-20	15	331	103	—
20-30	25	404	96	90
30-40	35	97	125	—
40-60	50	19	426	261
60-90	75	2	235	307
90-110	100	—	15	266
110-140	125	—	—	76
Totals		1000	1000	1000
Specific surface, S_0 cm. ² /cm. ³		2070	950	653
Average particle size, d_m		29 μ	63 μ	92 μ

Table II. *Permeability of spherical glass particles*

Material	Liquid	Viscosity η	Porosity ϵ	K_1 (observed)	K_1 (calculated)
Fraction I	Acetone	0.00415	0.338	4.24×10^{-8}	4.03×10^{-8}
	Acetone	0.00415	0.360	4.98×10^{-8}	5.18×10^{-8}
	Alcohol	0.0154	0.360	4.95×10^{-8}	5.18×10^{-8}
	Alcohol	0.0154	0.370	5.62×10^{-8}	5.82×10^{-8}
Fraction II	Acetone	0.00415	0.390	3.19×10^{-8}	3.46×10^{-8}
	Alcohol	0.0154	0.384	3.09×10^{-8}	3.23×10^{-8}
Fraction III	Acetone	0.00415	0.375	6.25×10^{-8}	6.19×10^{-8}
	Alcohol	0.0154	0.392	7.41×10^{-8}	7.5×10^{-8}

In the case of small, irregular particles, it is not possible to measure S_0 accurately by examination under the microscope, but, if equation (4a) is accurate, it should be possible to calculate S_0 for two powders, by measuring K_1 for each, and then to calculate K_1 for any mixture from the values so obtained.

Two quartz powders, tested in this way, gave $S_0 = 22,500 \text{ cm.}^2/\text{cm.}^3$ (or $d_m = 2.7 \mu$), and $S_0 = 6340 \text{ cm.}^2/\text{cm.}^3$ (or $d_m = 9.4 \mu$), respectively. When mixed in equal proportions, the calculated specific surface should be $\frac{1}{2} (22,500 + 6340) = 14,400 \text{ cm.}^2/\text{cm.}^3$. Two tests on the permeability of the mixture gave

ϵ	$K_1 \times 10^7$ (observed)	$K_1 \times 10^7$ (calculated)
0.436	2.32	2.47
0.456	3.06	3.03

In another series of experiments, mixtures of a highly purified grade of kieselguhr, with a porosity $\epsilon = 0.849$, were made with samples of the second quartz powder, the porosity of which was 0.47. The values of S_0 , obtained from the permeabilities, were, respectively, $17,200 \text{ cm.}^2/\text{cm.}^3$, ($d_m = 3.5 \mu$), and $6340 \text{ cm.}^2/\text{cm.}^3$, so that a mixture containing a fraction, x , by volume of the kieselguhr, should have a specific surface given by

$$S_0 = 6340 \times (1 - x) + 17,200x \\ = (6340 + 10,770x) \text{ cm.}^2/\text{cm.}^3$$

Table III. *Permeabilities of mixtures of kieselguhr and quartz powder*

x (volume fraction of kieselguhr)	ϵ porosity	$\epsilon^3/(1 - \epsilon)^2$	$K_1 \times 10^5$ (observed)	$K_1 \times 10^5$ (calculated)
0.00	0.470	0.37	0.181	—
0.020	0.485	0.43	0.203	0.196
0.044	0.530	0.675	0.299	0.282
0.123	0.607	1.45	0.462	0.484
0.262	0.670	2.76	0.631	0.645
0.400	0.721	4.82	0.762	0.83
0.495	0.751	6.74	0.895	0.97
0.740	0.806	13.9	1.31	1.33
0.900	0.831	20.1	1.49	1.53
1.00	0.849	26.6	1.76	—

In Table III, there are given observed values of K_1 , and the values calculated from these values of S_0 . The two constituents were chosen to provide a wide range of porosity, and the range of the porosity function, $\epsilon^3/(1 - \epsilon)^2$, is shown in Table III. The agreement between the calculated and the observed values of K_1 shows undoubtedly that this function expresses the true relation between porosity and permeability.

MODIFICATION OF KOZENY'S EQUATION FOR CLAYS

Although, in most cases, experiment is overwhelmingly in favour of Kozeny's theory, this does not appear to be the case for clays. This is well shown by an important series of experiments by Zunker (1932), who investigated the permeabilities of a certain heavy clay soil over a wide

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range of porosities. The data are given in the first two columns of Table IV, and, in the second last column, there is the ratio of K_1 to the porosity function, $\epsilon^2/(1-\epsilon)^2$. According to Kozeny's theory, this should be a constant, but, instead, it is apparent that K_1 decreases very much more rapidly than the porosity function. Similar observations have been obtained more recently by Macey (1938), so that the behaviour, in a greater or less degree, seems to be common to all clays.

Table IV. *Zunker's data on permeabilities of a clay soil*

$K_1 \times 10^{10}$	ϵ	$= \epsilon - [0.262 (1 - \epsilon)]$	$K_1 \times 10^{10}$ $\times (1 - \epsilon)^2 / \epsilon^2$	$K_1 \times 10^{10}$ $\times (1 - \epsilon)^2 / \epsilon_1^2$
9.72	0.591	0.484	7.87	14.3
8.94	0.587	0.479	7.47	13.9
9.66	0.582	0.472	8.52	16.1
7.42	0.562	0.448	7.98	15.8
2.89	0.503	0.373	5.62	13.8
2.10	0.479	0.342	5.20	14.3
1.65	0.460	0.319	4.94	14.8
1.23	0.443	0.298	4.38	14.4

Owing to its great importance with respect to the permeability of soils, this behaviour of clays merits a detailed discussion. The evidence for Kozeny's theory is so strong that it appears reasonable to regard it as the "normal" law of permeability and therefore to seek some cause for the "abnormal" behaviour of clays. A first suggestion, which has been favoured by Terzaghi (1925) and by Macey, is that liquid viscosities in very narrow, capillary passages are higher than normal, and that viscosity increases as the diameter of the capillary decreases. This would give a qualitative explanation of the phenomenon, but does not lend itself to quantitative expression unless the relation between viscosity and capillary size is known. Such changes of viscosity, however, seem to be invalidated by the interesting experimental work of Bastow & Bowden (1935), for these workers have proved that viscosities of simple liquids show no sign of alteration in rectangular channels down to 1μ in width.

A more profitable suggestion was made by Zunker himself and later incorporated by Kozeny (1932) into an extension of his own theory. This was to assume that a film of water is held stationary at the surface of the clay particles, with the result that the effective pore space, in which water is free to flow, is reduced. An indication of the amount of water so held is given by what Zunker calls the "hygroscopicity" of the clay, i.e. the weight of water retained by 100 g. of clay (dry weight) when dried in a desiccator at 20°C . For the clay soil under consideration, the hygroscopicity was 7.53. Since the true density of the fully dried clay was 2.68 g./cm.^3 , this may be converted more conveniently for our present

purposes to 0.202 cm.^3 of water per 1 cm.^3 of solid volume. The hygroscopicity represents water bound so firmly by the clay that it has a negligible vapour pressure at 20°C. , and may therefore be regarded as giving a rough measure, probably on the low side, of the water bound so firmly that it remains stationary when percolation takes place. If the two quantities are equated, the free pore space, when the total pore space is ϵ , must be $\epsilon_1 = [\epsilon - 0.202 (1 - \epsilon)]$, since, in each 1 cm.^3 of the bed, there will be $(1 - \epsilon) \text{ cm.}^3$ of solid volume, and hence $0.202 (1 - \epsilon) \text{ cm.}^3$ of "hygroscopic water".

In modifying his theory, Kozeny (1932) substituted the free pore space ϵ_1 for the total pore space ϵ in equation (14), obtaining

$$K_1 = \frac{g}{k} \frac{\epsilon_1^3}{S^2}. \quad \text{.....(16)}$$

Thus, when one substitutes $S = (1 - \epsilon) S_0$, the modified equation becomes

$$K_1 = \frac{g}{k S_0^2} \frac{\epsilon_1^3}{(1 - \epsilon)^2}, \quad \text{.....(17)}$$

and the ratio of K_1 to the new porosity function $\epsilon_1^3/(1 - \epsilon)^2$ should be constant. Actually, to obtain constancy, as shown in Table IV, it was necessary to assume that the volume of the stationary film was 1.3 times that of the hygroscopic water, so that the expression for ϵ_1 became $[\epsilon - 0.262 (1 - \epsilon)]$. As pointed out above, this is quite reasonable, and leaves unaffected the main fact that the two quantities are comparable.

The average value of $K_1 \times (1 - \epsilon)^2 / \epsilon_1^3$ in the last column of Table IV is 14.7×10^{-10} , and, according to equation (17), this is equal to g/kS_0^2 or $196/S_0^2$, whence $S_0 = 3.65 \times 10^5 \text{ cm.}^2/\text{cm.}^3$ and the effective particle size is $d_m = 0.164 \mu$. It is thus possible to calculate the thickness of the stationary layer, for every cm.^3 of solid volume has a surface, $3.65 \times 10^5 \text{ cm.}^2$, and 0.262 cm.^3 of water in the stationary layer. The average thickness of the layer, δ , is thereby $7.2 \times 10^{-7} \text{ cm.}$, i.e. 72 Å., or about thirty molecular diameters. At first sight this appears rather excessive, but, in the past, layers of 1000 and 3000 Å. have been postulated to explain the plasticity of clays (Houwink, 1937). Although such excessive thicknesses are no longer considered probable, Mattson (1931) has shown that, when water is added to a dry clay soil, there is a definite heat of adsorption until the amount of water corresponds to a film of the order of 40 Å. in thickness. Further additions involve no further heat change. This is at least of the same order as δ .

Exactly in what form the water is retained is still not quite certain, since it is difficult to conceive of an adsorbed film exceeding 10 Å. The

more recent advances in the structure of clay minerals may possibly clear up this matter. Clay minerals are characterized by a layer structure in which there is a very strong resistance to rupture across the layers, but very weak forces holding the layers together. It is this which accounts for the typical shape of clay particles, namely, laminae in which the length and breadth greatly exceed the thickness. The most typical mineral in soil clays is beidellite (Marshall, 1936), which, as has been proved by Hofmann *et al.* (1934), is capable of a very large and indefinite degree of hydration between the layers, accompanied by a uni-directional expansion at right angles to the layers. The following visualization of Kozeny's modified theory seems therefore a reasonable one. One may imagine 1 cm.³ of the clay soil completely water free. The porosity is ϵ , and the particle surface, therefore, $S = (1 - \epsilon) S_0$. Since the particles are very thin laminae, this surface will be represented by the two flat sides of each laminae, for the contribution of the edges will be negligible. Water is next admitted to fill the pore space. Part of this is adsorbed strongly, while another part, several times greater, will hydrate the clay and cause the laminae to increase considerably in thickness. This swelling, together with the adsorbed layer, corresponds to a reduction in the effective pore space. Further, since an increase in thickness will not affect the flat surfaces of the laminae, the value of S will remain practically unchanged, i.e. it will still be equal to $S_0 (1 - \epsilon)$, where S_0 is the specific surface of the unhydrated clay. In other words, in transforming from equation (14) to equation (16), Kozeny is justified in assuming that the effective pore space is reduced from ϵ to ϵ_1 , while the value of S suffers no modification.

This viewpoint cannot be considered unless it can first be shown that the amount of swelling in each layer falls within reasonable limits. If the average laminar thickness is t cm., the specific surface S_0 is equal to $2/t$, and, conversely, t is equal to $2/S_0$, i.e. 0.55×10^{-5} cm., or 550 Å. Assuming a spacing of 12 Å. between layers for the unhydrated clay, this gives the average number of layers in a lamina as 45.5. Now suppose the whole of the water represented by the "stationary film thickness", δ , is used for hydration and swelling. Then, since this film is present on both sides of each lamina, the amount of swelling in each layer is $2\delta/45.5$, i.e. 3.2 Å., a value well within the limits suggested by the work of Hofmann *et al.* Thus, a sample of montmorillonite, which swelled in water till the spacing between layers was 19.6 Å., gave a spacing of only 9.6 Å. on drying at 350° C.

It is interesting to note that Mattson calculated his value of 40 Å. for the "adsorption film" by assuming $S_0 = 1.2 \times 10^6$ cm.²/cm.³. If one

carries out a similar calculation to the above, assuming the water is not adsorbed but used for hydration, the swelling in each layer amounts to 5.8 Å.

DATA OF TERZAGHI ON PERMEABILITY OF CLAYS

Apart from the data of Zunker, the only published data appear to be some measurements made by Terzaghi (1925), which are printed as a graph of rather small dimensions. The data given in Table V were read from an enlargement of this. These figures were read from experimental points, and not from the curves drawn through them, except in the case of the highest permeability and porosity for each clay. This last reading was justified, since, according to the text, the curves were drawn to pass through experimental points which lay outside the published graph, and which therefore represented higher porosities and permeabilities than any reproduced in Table V. The values of K_1 were calculated from Terzaghi's permeability coefficients on the assumption that the viscosity of the water corresponded to a temperature of 10° C. A point worth noting is that Terzaghi proved the validity of equation (1) (D'Arcy's law) for clays, since he obtained consistent permeabilities on varying both the thickness of the clay beds and the pressure gradient across them.

Table V. *Terzaghi's data on permeability of clays*

Clay	$K_1 \times 10^{10}$	ϵ	ϵ_1	$K_1 \times 10^{10} \times (1 - \epsilon)^2 / \epsilon^3$	$K_1 \times 10^{10} \times (1 - \epsilon)^2 / \epsilon_1^3$
A	2.4	0.56	0.36	2.65	10.0
	1.01	0.51	0.287	1.83	10.2
	0.35	0.46	0.214	1.05	10.4
	0.21	0.442	0.188	0.76	9.8
	0.13	0.425	0.163	0.56	9.9
	0.05	0.405	0.134	0.27	7.4
B	2.4	0.593	0.369	1.90	7.8
	0.62	0.524	0.262	0.98	7.9
	0.35	0.50	0.225	0.70	7.7
	0.24	0.486	0.203	0.55	7.7
C	2.4	0.42	0.287	10.9	34
	1.35	0.38	0.238	9.4	38
	0.51	0.338	0.186	5.8	35
	0.40	0.325	0.170	5.4	37
	0.07	0.284	0.119	1.6	21

$$\epsilon_1 \text{ for clay A} = \epsilon - 0.455(1 - \epsilon)$$

$$\epsilon_1 \text{ for clay B} = \epsilon - 0.55(1 - \epsilon)$$

$$\epsilon_1 \text{ for clay C} = \epsilon - 0.23(1 - \epsilon)$$

As shown in Table V, Terzaghi's data conform very well to Kozeny's modified theory, except, in the case of clays A and C, for permeabilities so small that their accuracy was doubtful, both in the original measurement and in the writer's attempt to read the plotted points from Terzaghi's graph.

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The values of S_0 for these three clays, calculated from the quantities in the last column of Table V, are, respectively, $4.4 \times 10^5 \text{ cm.}^2/\text{cm.}^3$ for clay A, $5.0 \times 10^5 \text{ cm.}^2/\text{cm.}^3$ for clay B, and $2.35 \times 10^5 \text{ cm.}^2/\text{cm.}^3$ for clay C. The corresponding values of δ are, therefore, 103, 110 and 99 A. If one carries out a calculation for the "average amount of swelling per layer", similar to that given for Zunker's clay soil, the values reached are 5.5 A. for clay A, 6.6 A. for clay B, and 2.8 A. for clay C. It is to be noted that clays A and B fall into a different class from clay C, and that the latter is in the same class as Zunker's clay soil. This is in accord with their nature, for, whereas clays A and B were pure plastic clays, clay C was little more than a "sandy mud", containing 59.1 % of sand, and Zunker's substance was a soil containing 51.8 % of particles over 2μ in diameter. The calculation of "average swelling per layer" is based on the assumption that the material is a pure clay, and it is undoubtedly true that, were it possible to make allowance for silica particles, and to calculate on the clay alone, the average swelling per layer would be of the same order as for the plastic clays.

A distinctive feature of Kozeny's theory is that the permeability becomes zero while the porosity has still quite a considerable value, namely, $\epsilon=0.207$ for Zunker's clay soil, and $\epsilon=0.313$, $\epsilon=0.355$ and $\epsilon=0.187$, respectively, for clays A, B and C. This is not brought out very well by Zunker's results, but Terzaghi's data show clearly how rapidly the permeability falls toward zero as the limiting porosity is approached.

. SUMMARY

It is shown that the permeability of a water-saturated sand or fine powder can be calculated with considerable accuracy, if the porosity and the specific surface are known. In particular, the Kozeny theory here discussed leads to a very useful relationship between permeability and porosity. It is shown that clays do not conform to the theory in its simple form, but that it may be modified to give a satisfactory representation of the data available. The physical grounds for this modified theory are discussed in some detail, and it is shown that, while it is open to criticism, it is at least in harmony with our present knowledge of clays.

An important deduction which follows from the modified theory is that clays may have zero permeability at quite considerable porosities, e.g. at $\epsilon=0.207$ for a clay soil, and $\epsilon=0.355$ for a plastic clay.

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ANALYSIS OF POST-WEANING GROWTH IN PIGS

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(With Three Graphs)

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INTRODUCTION

A CONSIDERABLE volume of recent work has made it clear that carcass quality is closely bound up with breed, strain and type of pig, and with rate of growth. In addition to the reports of the Scandinavian and German Pig Testing Stations, the investigations of Schmidt *et al.* (1934), French & Emson (1936), Lush (1936), Shaw & McEwan (1936), Kliesch (1937), McMeekan (1937), Hammond & Murray (1937) and others, agree in emphasizing the importance of genetic constitution. Rate of growth studies may obviously take a variety of forms. That which deals with the differential rates of development of muscle, fat, and bone has been greatly advanced by the long series of researches by Hammond (1932*a, b*), in which he has made it clear that even genetically similar animals cannot be expected to have the same carcass measurements unless they have been exposed to the same environmental conditions throughout

their growing period. Another form has been concerned directly with the effects of diet on carcass quality, the results of which have been reviewed by Callow (1935). Some types of diet can result in too much or too soft fat, and deficiencies of particular constituents appear to be more detrimental to quality than excesses. Woodman *et al.* (1936), for instance, could find little or no effect of their high protein rations on carcass quality, nor could McMeekan (1937) with a very different type of diet. A much less extensive examination of the influence of rate of growth on carcass quality has been made on standard rations, but the work of Petersen (1936) and Mansfield *et al.* (1937) shows that this factor must be taken into account.

The problem of growth rate in relation to age and weight may be resolved into determining the response of animals to variations in type of environment, or into determining the variations in response within a given environment. The latter alternative has been followed by Berge (1936) and Vecchi (1934), who observed the growth of pigs during restricted periods and noted that the faster growing of two breeds in the early stages became the slower growing during the later stages of the test period. That litters within a breed can be distinguished effectively by their growth rates over a range smaller than 40–200 lb. will be shown in this paper. If these differences are ultimately traced to genetic causes, an extension of the idea of breed precocity to strains within a breed will be possible. With the knowledge that fast growth is more desirable at some stages of development than at others, a more satisfactory avenue for selection would be opened up, together with a promising application of the growth and form theory linking growth rates and carcass quality.

In the present work existing variation in the growth of bacon pigs has been studied in some of its aspects, with the object of deciding whether further analysis on these lines is likely to prove profitable. This is necessarily the first step. The next is to determine whether the observed litter differences are heritable and whether they are accompanied by corresponding carcass differences. This report becomes, therefore, a consideration of the variation in growth during certain defined periods, with special emphasis laid on the relation between the gains made during successive periods. With this definition of its scope, the opportunity has been taken of including some reference to the significance of weaning weight. The emphasis placed on the importance of heavy weaners has led to some misapprehension as to the meaning of the underlying correlations between weaning weight and subsequent growth. As a practical step towards more economical production, the raising of average

weaning weights has a clearly established value, but insistence on the correlation of weaning weight with subsequent growth has the disadvantage that it focuses attention on the weaner rather than on the important factor in rearing heavy weaners—the milk production of the sows.

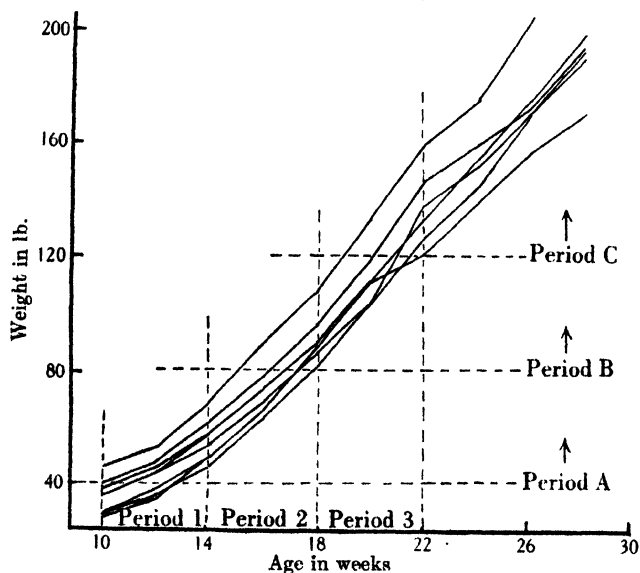
MATERIAL AND METHODS

The material for this investigation has been provided by the observations made since 1931 on the Large White herd of pigs maintained by the Institute of Animal Genetics at Edinburgh. The type of management and the rations for all classes of stock have been unchanged throughout with the exception of an alteration in the feeding of dry sows at the end of the first year. Litters were weaned at 8 weeks and thereafter weighed fortnightly, and fed quantities of a standard ration determined by the amounts eaten promptly on the first day of each fortnight. Litters were raised complete—a method which enabled the food consumption to be calculated, but may have been disadvantageous to light weight members of a litter.

The principal part of this work has been the study of the variance and covariance of the increases in weight put on by the pigs during three periods of 28 days. In section A of this paper, these were 10–14, 14–18 and 18–22 weeks. The growth of each litter was graphed to permit easy interpolation where the weighing days did not coincide with the ends of the periods, and to indicate clearly erroneous weighings. A pig's weight is, of course, constantly changing, and any practicable method of dealing with large numbers of animals can only give an approximation to the actual gains in weight. Periods of 28 days were chosen partly in order that the errors of weighing should not be large in proportion to the weight increase, and partly to ensure at least three subdivisions of the growth curve.

In section B of this paper, a different method of fixing the 28-day periods has been used, in order to determine what alteration takes place in the variability when increases from the same weight are considered instead of the increases from the same age. Graph 1 shows a litter record subdivided vertically into three periods in which the pigs are all the same age, and horizontally into three periods in which the pigs all begin at the same weight. To distinguish the two type of periods, those beginning at a constant age are called periods 1, 2 and 3, while those beginning at a constant weight are called periods A, B and C. A slight modification of periods A, B and C was also used, which will be described later.

The gains shown by the individuals of a litter in any period were summed and averaged to give the "mean increase". From the sums of squares of the individual gains, the variance of the gains, $Sx^2/(n-1)$, was obtained for each litter, and is referred to as the "mean square". No distinction has been paid to sex, since Berge (1936) and Woodman *et al.* (1936) found only a slight difference over the whole test period, and the conditions of the present investigation did not warrant the



Graph 1. Growth curves for a litter of six pigs from 10 weeks of age, showing the method of subdivision into periods defined by age and weight.

refinement of separating the sexes. It is possible, therefore, that neglect of sex differences may have obscured the results to a slight extent.

For the study of the variability of the increases, the method adopted has been to analyse the variance of the mean square together with its covariance with the corresponding mean increase per litter. To assume that the variability would be proportional to the increases was considered inadvisable, and the method of analysis of Day & Fisher (1937) which avoids this assumption was applied.

A. Periods defined by age

The mean increase in weight per pig and its variation.

The mean increases in weight per pig per litter and their associated mean squares have been classified into groups according to period, litter

size and average weight of litter at weaning. The averages for these groups are contained in Tables I and II. Although there is a tendency for the mean square to be greater when the increase per period is greater, the relation between the two as determined by litter size groups is far from being regular. While the increase per pig remains fairly constant in each period from one litter size to another, the mean square varies considerably but not regularly with change in litter size. The relation between mean increase and mean square for the weaning weight groups seems clear. With the exception of the mean squares for the rather small group with the heaviest weaning weight in the second and third periods, the values in Table II change regularly in such a way that in each period a lowering of the weaning weight is associated with a reduction of the mean increase and with higher values for the mean square (see Graph 2). That is to say, with the periods defined as they are, litters heavy at weaning time tend to have a greater rate of growth and a lower mean square than lighter litters.

Table I. *Mean increase in weight in pounds per pig per litter and corresponding mean square classified according to period and litter size to nearest whole number*

Litter size ...	6		7		8		9		10		11		12		Average	
	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.
Period 1	23	35	24	22	21	36	22	36	21	26	22	31	20	32	22.0	31.0
Period 2	31	31	29	38	30	33	29	49	30	36	29	40	28	43	29.2	39.3
Period 3	35	51	35	39	34	50	36	51	37	34	32	49	34	37	35.1	46.0
No. of litters	10		26		27		32		19		13		8		135	

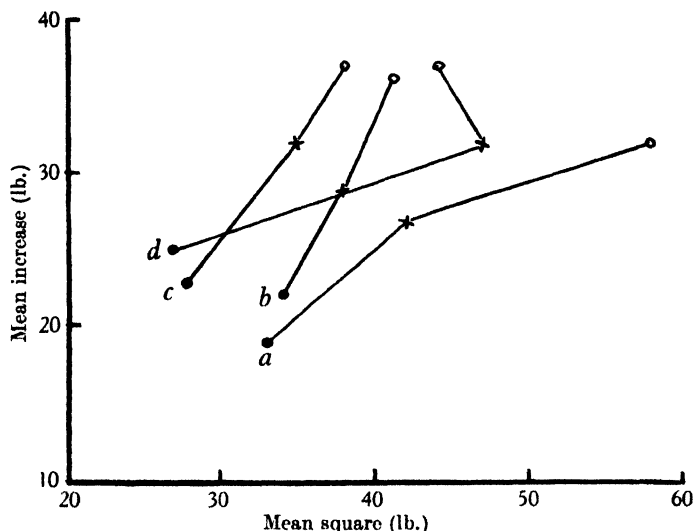
Table II. *Mean increase in weight in pounds per pig per litter and corresponding mean square classified according to period and weaning weight to nearest whole number*

Weaning weight ...	22 ± 2		26 ± 2		30 ± 2		34 ± 2	
Period	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.	M.I.	M.S.
1	19	33	22	34	23	28	25	27
2	27	42	29	38	32	35	32	47
3	32	58	36	41	37	38	37	44
No. of litters	40		40		37		18	

Since the amount of variation within and between litters is so large it is unsafe to draw any definite conclusions from the averages given above. Statistical analyses have therefore been made in order to estimate the importance of those sources of variation which most

probably have had a real effect on the increases and their mean squares. Table III shows the relative importance of periods, litter sizes and weaning weights on the mean increase in weight per pig during 28 days.

From these figures it appears that the mean increase in weight per pig is substantially affected by its weaning weight as well as by the period in which the growth takes place. These results are entirely to be



Graph 2. Effect of weaning weight and period on the relation between mean increase in weight and its variability (mean square).

Period	Weaning weight
1 —●—	a 22 ± 2 lb.
2 —×—	b 26 ± 2 lb.
3 —○—	c 30 ± 2 lb.
	d 34 ± 2 lb.

expected. The normal growth curve of a pig shows (Berge, 1936) that the absolute rate of increase in weight becomes faster until bacon weight is approached. The heavier a pig is at weaning, therefore, the faster will it tend to grow in all periods. Litter size has had no effect on the increase.

A similar analysis for the mean square for each litter is given in Table IV.

Period and weaning weight class again had real effects, the mean square increasing from first to last period, and decreasing as weaning weight increased (Tables I and II). The influence of litter size was again

without significance. None of these three variables was really effective in controlling the observed variation. Even by removing the variance due to period, the mean square was reduced by less than 5%, whereas the same process applied to the variance in mean increase reduced the mean square by 44% (see Table III).

Table III. *Analysis of variance of the mean increase per pig during 28 days*

	Sum of squares	D.F.	Mean square	Significance
Total	25847	400	64.6	
Between periods	11473	2	5736.5	S.S.
Within periods	14374	398	36.1	
Between litter sizes within periods	441	18	24.5	N.S.
Within litter sizes and periods	13933	380	36.7	
Between weaning weights within periods	1926	9	214.0	S.S.
Within weaning weights and periods	12448	389	32.0	

N.S. non-significant; S.S. significant at 1% point.

S. significant at 5% point.

Table IV. *Analysis of variance of the mean square deviation for each litter*

	Sum of squares	D.F.	Mean square	Significance*
Total	308518	400	771.3	
Between periods	15265	2	7632.5	S.S.
Within periods	293253	398	736.8	
Between litter sizes within periods	14934	18	829.7	N.S.
Within litter sizes and periods	278319	380	732.4	
Between weaning weights within periods	12894	9	1432.7	S.
Within weaning weights and periods	280359	388	722.6	

* As in Table III.

The variability of individual increases in weight.

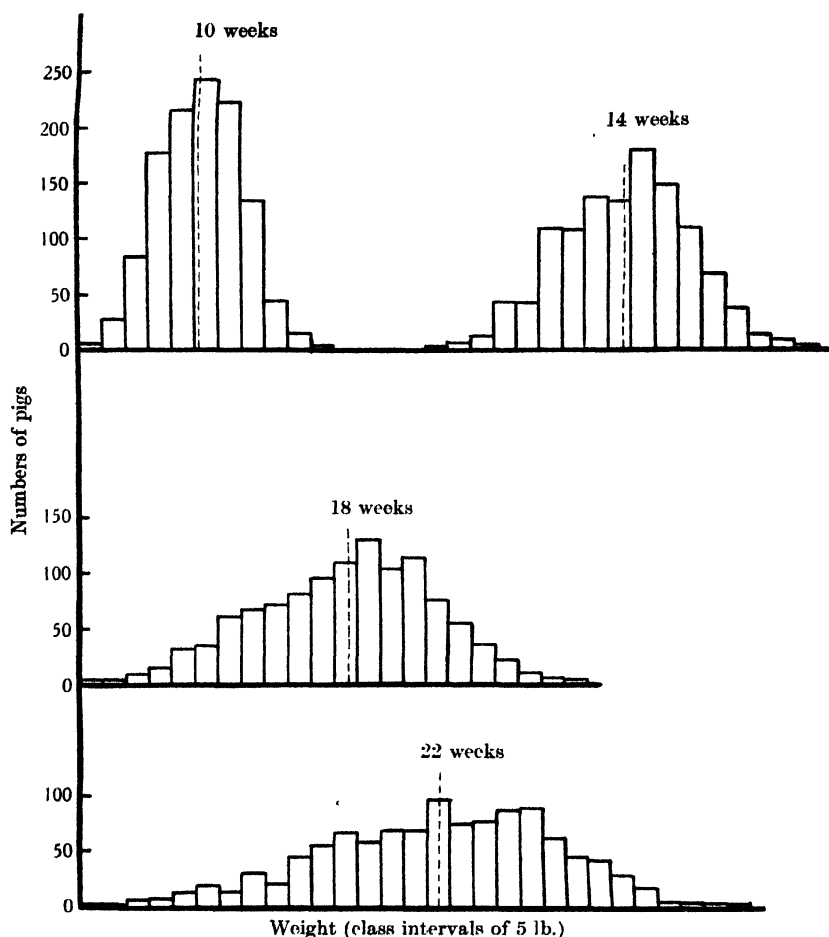
The factors which have been shown to influence the variability of the increases (in the preceding section) may do so through their effect on the increases themselves. Lacking evidence on the point, it might be assumed that as the increase in weight becomes larger, its variance is augmented in proportion. This assumption is made if the variabilities are compared by means of the coefficient of variability. In fifteen out of the twenty-one groups of Table I, however, the covariance of the mean increase with the mean square was negative, and the assumption becomes of very doubtful validity. On the contrary, it appeared as though there was a tendency within each subdivision of the data for the mean square to diminish as the mean increase became larger.

Following graphical examination of the covariances of the mean squares and mean increases, the linear regressions of the former on the latter were estimated by calculating coefficients, as follows:

Within periods	-1.206 ± 0.226
Within litter sizes	-0.172 ± 0.172
Within weaning weights	-0.042 ± 0.177

Of these coefficients, only that within periods is significant. The regression is such that for each pound by which the mean increase enlarges, the mean square diminishes by 1.206. Since the regression within weaning weight classes is negligible, it seems probable that weaning weight differences account for the regression within periods. This means, in effect, that the fast-growing litters were less variable than the slow-growing litters. At first sight this appears to be incompatible with Hammond's conclusion (1932*b*), that the greatest variability occurs during periods of the greatest growth rate, but both are true for the present data. In Table I it is shown that in passing from period 1 to period 3 the mean square becomes greater—which is in accord with Hammond's results. Such a result is to be expected, since the older animals have been exposed longer to a fluctuating environment, and also have a greater range of possible growth rates within which they can vary. This treatment of the data involves comparisons of all the animals at three separate ages.

If subgroups of animals are compared at the *same* ages, a different result is obtained. The fast-growing animals are less variable than the slow growing. The explanation of this, it is suggested, is that litters of high average weight which are near to the maximum rate of growth possible at the given age, respond only slightly to further favourable environmental influences, and are not much affected by unfavourable influences, whereas litters of low average weight can respond greatly to stimuli in either direction. A consequence of this is that the distribution of ages at a given weight (Berge, 1936), or weight at a given age is markedly skew. It is relevant in this connexion to recall that Kapteyn (1903) discussed the occurrence of skew curves in biology and suggested that they might be made into normal curves by the use of a suitable transformation whenever the skewness was due to a regular change in the variable by which the organisms were measured. Whether such a regular change accounts for all the skewness apparent in the distributions shown in Graph 3 may be doubted. The distributions were obtained by classifying the weights of animals at the ages of 10, 14, 18 and 22 weeks,



Graph 3. Frequency diagrams showing distribution of pigs in weight classes at the ages of 10, 14, 18 and 22 weeks. The means are shown by dotted lines, the actual values being given in Table V.

Table V. Table showing the characteristics of the frequency distributions of the weight of pigs at intervals during growth. With the exception of the means, the values given apply to the arbitrary units of 5 lb.

Weeks old	10	14	18	22
Mean (lb.)	35.77	58.00	87.27	122.24
s.d.	1.76	2.75	3.79	5.01
$\sqrt{\beta_1}$	-0.0067	-0.0956	-0.2199	-0.2712
β_2	2.611	2.685	2.660	2.709
No. of pigs	1168	1143	1126	1098

and their descriptive statistics are given in Table V. The skewness, although not apparent at 10 weeks, becomes marked as the age increases. The observed skewnesses are 0.1, 1.3, 3.0 and 3.6 times their standard error (0.074 for $N=1100$), so that the last two are significant. Similarly, the 5% value for the coefficient β_2 is about 2.76, so that all the observed values indicate a significant degree of flattening.

Whether a certain amount of skewness should be anticipated in the distribution of weights from a population of pigs need not be debated here. Most of the long negative tail actually observed can be traced to animals of subnormal growth at some time, animals which are growing at a rate commensurate with their weight rather than with their age (as will be shown later). These may be regarded as a separate population with characteristics different from those of the principal group. At any age their mean weight and growth rate are well below the average and consequently when combined with the principal group they contribute only to the negative side of the distribution. The increasing degree of skewness ($\sqrt{\beta_1}$) can be accounted for, since the increasing absolute rate of growth places the unchecked pigs relatively further and further ahead of the slower growing group.

From this brief examination of the changes in magnitude of variability under group feeding conditions, it may be reasonably deduced that the practice of allotting pigs to feeding groups according to weight is well founded. With this arrangement, the tendency for large discrepancies in weight to develop is checked at the outset, and a better control of individual growth rates is possible. Those who are interested in the growth rates and food consumptions of litters, however, cannot use this method. For them it seems likely that the advantages of decreasing variability, by reducing litters to a more or less even sample as small as four (Smith & Donald, 1937), will more than offset the loss of information involved by excluding members of the litters.

Relations between increases in weight in different periods.

The changes in variability noted above, although making the discovery of inter-litter differences more difficult, would not necessarily alter relative performances, as judged by the litter means. That they are, in fact, altered is shown by the correlations between the mean increases in different periods given in Table VI. Correlations between individual increases have not been calculated for the periods defined by age, and it cannot be assumed that they would be similar to those appropriate to the means. The coefficients of Table VI have been calculated for

various relationships of the four quantities—the means and their sum for the three periods, p_1 , p_2 , p_3 and P .

From these figures it will be noted that (1) litter size does not affect the coefficients; in fact, those for litter sizes 7, 8, and 9 are remarkably similar; (2) as befits their large contributions to the total, the increases in p_2 and p_3 are both strongly correlated with the total increase; (3) the influence of p_1 on P is smaller than that of p_2 and p_3 and is exerted mainly through its effect on p_2 ; (4) although $r_{p_2 p_3}$ is about +0.6, the partial correlations $p_2 P.p_3$ and $p_3 P.p_2$ are not greatly different from

Table VI. *Correlation coefficients for relation between average litter increases in different periods*

p_1 , first period; p_2 , second period; p_3 , third period; $P = p_1 + p_2 + p_3$; n , number of litters

n	Litter size					
	6	7	8	9	10	11
	11	26	29	35	13	12
$p_1 P$	+0.69	+0.63	+0.57	+0.62	+0.48	+0.27
$p_2 P$	+0.84	+0.87	+0.83	+0.82	+0.93	+0.81
$p_3 P$	+0.94	+0.90	+0.83	+0.81	+0.87	+0.80
$p_1 p_2$	+0.44	+0.45	+0.37	+0.40	+0.45	+0.03
$p_1 p_3$	+0.51	+0.37	+0.19	+0.18	+0.04	-0.14
$p_2 p_3$	+0.69	+0.66	+0.50	+0.50	+0.72	+0.48
$p_1 P.p_2$	+0.66	+0.56	+0.51	+0.55	+0.17	+0.43
$p_1 P.p_3$	+0.73	+0.76	+0.74	+0.82	+0.90	+0.66
$p_2 P.p_3$	+0.78	+0.85	+0.87	+0.83	+0.90	+0.82
$p_2 P.p_1$	+0.92	+0.88	+0.87	+0.82	+0.79	+0.81
$p_3 P.p_1$	+0.83	+0.82	+0.84	+0.79	+0.91	+0.84
$p_3 P.p_2$	+0.94	+0.87	+0.89	+0.91	+0.97	+0.89

the total correlations $p_2 P$, and $p_3 P$; (5) eliminating the influence of p_1 has not greatly altered the correlation of p_2 and p_3 with P . There is thus a considerable degree of similarity in the performances of different periods. A correlation of +0.6 ($r_{p_2 p_3}$) is, however, far from being as large as desirable between two consecutive periods of 28 days, if the whole test period is to provide a reliable measure of breeding value. The circumstances giving rise to a coefficient of +0.6 must involve a considerable number of fluctuations in growth produced by influences either external or internal, or both. In so far as environment could be more strictly controlled at a testing station, these results constitute a justification of testing, for if the tested animals are themselves responsible for some of the relative differences in performance, the chances of detecting such differences would be greatly enhanced. Litters could, of course, not be judged solely by some standard such as growth rate per day from start of test. The best litters are then those with good performance in

all periods. This may appear to be all that is required, but, looking at the question from the point of view of carcass quality, another point arises. If it is proved that quality of carcass is associated with relatively slow growth in the latter stages, it would then become necessary to distinguish animals of this type from others having the same average over all performance, but showing comparatively slow initial growth followed by rapid fattening.

Under Edinburgh conditions, the performance of the litters in period 1, that is from 10–14 weeks of age, has shown a rather low correlation with subsequent performance, and must therefore have tended to obscure the inter-litter differences subsequently manifested. If it may be assumed, for practical purposes, that the immediate post-weaning history of a litter is without significance from the genetic standpoint, it would seem advisable to exclude from litter comparisons the data obtained from pigs which have not clearly adapted themselves to solid feeding. This is the procedure adopted for testing stations, and with good reason. It amounts to discounting that portion of the growth which may be directly or indirectly attributed to the uncontrolled nutrition whilst on the mother, since the length of the period to be disregarded will depend on the weaning weight. Evidence that it may be disregarded without affecting the subsequent results is offered in the ensuing section of this paper in which the pigs are compared on a weight instead of an age basis.

B. Periods defined by weight

Inter-litter differences.

The foregoing method of treatment of growth rate data gives results which depend on the actual performance of litters during specified periods which are the same for all pigs in all litters. It is a consequence of this that pigs which are small for any reason at the beginning of a period, are at a disadvantage throughout when absolute and not relative growth rates are considered. Litter averages and correlations which describe the performance of animals over long periods of their lives (e.g. average number of days from weaning to slaughter, correlation between weaning weight and growth rate from weaning to bacon weight) take no account of checks of various kinds, and no account of the relative but irrelevant disadvantage of the small pig, whose size may be merely a reflection of his dam's milking capacity. By the technique of calculation, it comes about that all environmental checks to growth are combined with any real genetical inferiority or superiority which may thus be effectually obscured.

These remarks may be illustrated by analyses made of the litters available in litter sizes 8 and 9. For these litters, the weaning weight has been compared with the actual increase in weight put on during three periods of 28 days each as before. In contrast to the previous calculations, the periods were chosen for each pig independently in such a way that the first (period A) began when the pig reached 40 lb. weight. Since growth curves were available for each animal this was readily done (see Graph 1). For litter size 8, period B began when the pig reached 80 lb., and period C when it reached 120 lb. For litter size 9 on the other hand, the end of period A became the beginning of period B, and so on. With the former method there was slight overlapping of periods when more than 40 lb. was put on during the first and second periods. From Table VII it will be seen that the average increase for the second period was 37.66 ± 5.54 , so that rather more than a sixth of the pigs were allotted slightly overlapping periods. There is so little difference in the actual growth rates of the second and third periods that this overlapping cannot be of much importance. In both groups, allowances were made for obvious checks in the growth rate to avoid including periods of very slow or no growth. The object was to obtain a fair estimate of the growing capacity and in making any adjustments, the general trend of the growth curve was considered and not any brief periods of fast or slow growth. The checks were by no means confined to the smallest pigs, and sometimes involved whole litters. The post-weaning check was in evidence, but was usually over by the time the pigs reached 40 lb.

A comparison of the means for each period, together with an analysis of the variance is available in Table VII.

The differences between the means of corresponding periods are too small in comparison with the standard deviations to be significant. Litter size may therefore be presumed to have been unimportant here. The most interesting feature of the table is the undoubted significance of the difference between litters in all the periods including the suckling period. In all cases, the chances that the observed differences are purely random are much less than 1 in a 100. Weaning weight, as might be expected, is subject to relatively greater inter-litter differences than the other weight increases. Doubtless they are affected more by seasonal changes than the latter, but allowing for this, an undesirable amount of variation existed in the quality of the sows.

Table VII may lead to the supposition that litters could be easily distinguished. Obviously litter mates must tend to resemble each other more than they resemble non-litter mates, or else there would be no

Table VII. *Mean weaning weight and increases in weight in pounds per pig during three 28-day periods for 29 litters of 8 pigs and 31 litters of 9, together with corresponding analyses of variance*

		Litter size 8							
		Weaning weight (w)		Period A (x)		Period B (y)		Period C (z)	
Means		27.1 ± 4.98		25.24 ± 4.52		37.66 ± 5.54		42.00 ± 6.16	
Variance	D.F.	Sw ²	Mean square	Sx ²	Mean square	Sy ²	Mean square	Sz ²	Mean square
Total	231	11,465	49.6	5,566	24.1	8,322	36.0	11,377	49.3
Between litters	28	6,417	229.2	1,422	50.8	2,094	74.8	3,668	131.0
Within litters	203	5,048	24.8	4,144	20.4	6,228	30.7	7,709	38.0
F (1 % point about 1.8)			9.2		2.5		2.4		3.4

		Litter size 9							
Means		28.20 ± 5.58		25.85 ± 5.09		33.75 ± 6.23		40.31 ± 6.97	
Variance	D.F.	Sw ²	Mean square	Sx ²	Mean square	Sy ²	Mean square	Sz ²	Mean square
Total	278	14,475	52.1	9,002	32.4	14,540	52.3	18,509	66.6
Between litters	30	6,757	225.2	2,572	85.7	4,911	163.7	6,459	215.3
Within litters	248	7,718	31.1	6,430	25.9	9,629	38.8	12,050	48.6
F (1 % point about 1.8)			7.2		3.3		4.2		4.4

inter-litter differences, but that the degree of resemblance is not very strong follows from the intra-class correlations calculated from Table VII. The coefficients being small, indicate that within litters the pigs did not vary much less than all pigs regardless of litter. They are as follows:

		Intra-litter correlations based on		
		Increase during period		
Litter size	Weaning weight	A	B	C
8	+0.50	+0.15	+0.15	+0.23
9	+0.40	+0.20	+0.26	+0.27

An exception should be made of the correlations based on weaning weight from which it is apparent that there was a fairly considerable resemblance between litter mates. Such correlations bring out clearly the difficulties with which selection for growth rate is faced. Even if it could be arranged that all pigs in a litter had the same weaning weight, their subsequent growth to bacon weight, under conditions similar to those at Edinburgh, would still yield an intra-litter correlation of the order 0.15 (Smith & Donald, 1937).

Influence of weaning weight on subsequent growth.

The question now arises whether the later differences are associated with the initial differences established by weaning weight. Correlation

coefficients expressing the degree of relationship have therefore been calculated and are shown in Table VIII.

With one exception, the correlations between weaning weight and the weight increases during any of the three periods were insignificant. The exceptional case is difficult to understand, since it indicates the existence of a correlation between weaning weight and the increase in period B (litter size 8), although apparently the first and third periods were independent of weaning weight. Since the correlation between the means of the litters is fairly large, although itself insignificant, some adventitious association of means for weaning weight and increase in

Table VIII. *Correlation between weaning weight and increase in weight during three periods defined by initial weight*

(Litter size 8, 232 pigs; litter size 9, 279 pigs)

Weaning weight and increase in weight during	Calculated from	Litter size	
		8	9
Period A	All pigs	-0.057 N.S.	-0.065 N.S.
	Litter averages	-0.204 N.S.	-0.004 N.S.
	Pigs within litters	+0.035 N.S.	-0.103 N.S.
Period B	All pigs	+0.172 S.S.	-0.020 N.S.
	Litter averages	+0.299 N.S.	-0.097 N.S.
	Pigs within litters	+0.104 N.S.	+0.031 N.S.
Period C	All pigs	+0.079 N.S.	-0.101 N.S.
	Litter averages	+0.264 N.S.	-0.253 N.S.
	Pigs within litters	-0.060 N.S.	+0.001 N.S.

N.S. non-significant; S.S. significant at 1% point.

period B may have contributed enough to the total covariance to make a significant correlation. The signs of the coefficients are not consistent, and it must be concluded that these data contain no satisfactory evidence that either litters or pigs showed a growth rate which was influenced by their weaning weights. As can be seen from the variance of the means, the range of average weaning weights was rather large, and should have been adequate to discover any reasonably substantial effect.

Relation between the increases in weight in different periods.

Under this heading in the previous section it was observed that the correlation between the mean increases in the second and third periods was of the order of 0.6. With the restricted data available for this section, it has been possible to extend the correlation to the individuals within the litters, and to determine how far the observed differences in period B account for the differences in period C. This has been done by

adjusting the variance of the increases in period C in accordance with the covariance of the increases in periods B and C after the manner of Fisher (1936). In this way an estimate of the residual variance in weight increase in period C freed from the effects of the existing variation in period B was obtained.

The adjusted sums of squares for the total variance and the variance within litters for period C were not substantially different from the unadjusted values, but the variance between litters was reduced by about one quarter. The interdependence of the increases in periods B and C is described by the correlation coefficients given in Table IX.

Table IX. *Coefficients of correlation between increases during periods B and C*

	Litter size 8	Litter size 9
All pigs	+0.163 S.	+0.335 S.S.
Pigs within litters	+0.038 N.S.	+0.279 S.S.
Litter averages	+0.477 S.S.	+0.444 S.
No. of litters	29	31

From this Table it may be concluded that the differences between litters in the third period arose largely in that period and were not foreshadowed accurately by the increases in the second period. There was, nevertheless, a distinct tendency for increases in the two periods to be associated. To judge by the correlation coefficients, there was a stronger association between the litter means for the two periods than between the individual weight increases. In fact, when the increases were calculated from a constant weight, as with litter size 8, the latter correlation disappeared just as it did between weaning weight and increase in the first period, calculated from 40 lb. In the group of litters with nine pigs, the third period began where the second ended, and consequently any pig which grew slowly in its second period was handicapped by its small size and absolute growth rate when it entered its third period. The correlation of +0.279 within litters of nine is regarded as having much the same meaning as the correlations between weaning weight and subsequent growth measured from the weaning weight itself.

The correlation between means of litters gives no hint of its origin. It is perhaps rational to suppose that a genetically superior litter in period B may remain genetically superior during period C, but since so little of the variation in C is accounted for by regression of C on B, the weight increases are obviously very susceptible either to a fluctuating

environment, or possibly to the action of hereditary factors just commencing to operate, as, for instance, genes for late or early maturity. The correlations between means of litters given in Table IX, namely, $r=0.477$ and 0.444 for litter sizes 8 and 9, may be compared with the corresponding values in Table VI, $r=0.50$ for both litter sizes. In spite of the different methods of defining the periods, there is substantial agreement in the estimate of the relation between the increases in weight obtained in the two successive periods concerned.

DISCUSSION

In starting this particular investigation, it was felt that two of the chief difficulties in the way of determining the breeding value of pigs for bacon production were lack of knowledge concerning the sources of variation, and a tendency to regard growth rate, economy of gain or carcass quality, as simple genetic characters with complicated modes of inheritance rather than as complicated characters with components of simple modes of inheritance. Scientific poultry breeding for egg production now consists in the synthesis of genetic factors such as those for egg size, persistency, early maturity and stamina—a system which has proved more satisfactory than breeding on a basis of annual egg numbers. In the same way, the study of milk yield in terms of yields of fat and protein, different types of lactation curve, annual and lifetime productions, is the essence of the present trends of research.

The changes in rate of maturity induced in livestock during their evolution, and the influence of breed in determining age at "finished" weight, permit the inference that the rate and composition of growth are subject to some degree of genetic control. Schmidt *et al.* (1934) demonstrated with breed crosses, and Lush (1936) with the results of Danish progeny testing, that this control is sufficiently variable to offer considerable scope for selection in pigs. In order to make selection more effective, however, some improvement in the judging of genotype from observed performance is urgently required. The improvement may possibly come from a greater degree of subdivision of the growing period. If significant differences in the growth of litters are found in one period which are independent of the differences occurring in a previous period, it may be inferred that genetic differences of the type noted by Berge (1936) and Vecchi (1934) in their breed comparisons are involved. Such an inference is, of course, to be regarded with considerable suspicion until submitted to further experiments designed to test the possibility

that environment is wholly responsible. Genetic variation of this kind, if demonstrated beyond doubt, would be important in investigations of carcass quality and economy of gain.

The decrease of variability observed as the rate of growth increased may be regarded as evidence that equal environmental stimuli do not have equal effects on the growth rate of at least some of the animals. Under the system of group feeding practised, it is inevitable that some pigs will have secured a greater share of the rations than some of their litter mates, but if quantity of food is the principal factor governing the rate of increase, it is probable that when the litter, as a whole, is growing rapidly differences in food consumption will have a smaller effect than would the same differences in a more slowly growing litter. In other words, those animals which are growing at or near their maximum rate respond less to stimuli in either direction than those which are still far from the maximum. Comparable results were obtained by Donald (1937) with suckling pigs which did not show at all levels of nutrition equal increments of weight for equal increments of milk. This relation between variability and growth rate may conceivably come to have some importance, for genetic variation may be most marked at levels of feeding which are not optimal for the production of best quality carcasses.

In a previous paper it has been shown (Smith & Donald, 1937) that weaning weight has a very definite influence on the subsequent rate of growth of bacon pigs, as measured from time of weaning. This is entirely in agreement with the published observations of many workers in various countries. It was pointed out in the same paper, however, that the resemblance in growth rate of pigs of the same weaning weight (as measured by intra-class correlation) was very slight. This was taken to mean that weaning weight considered without relation to other factors, such as the weights of litter mates, was a poor guide to subsequent performance. Similar conclusions have been arrived at by Husby (1933), Wenck (1931), Berge (1936), Schmidt & Zimmermann (1934) and Menzies-Kitchin (1937). That the ordinary correlation between weaning weight and subsequent growth is more a statistical than a biological conception can be demonstrated by defining the subsequent growth periods by initial weight instead of initial age. In the preceding pages, both methods have been used. The former yields no significant correlation, while the latter does. The difference is due to the inclusion in the calculations by the latter method of the time necessary for the light weaners to put on the deficient weight at weaning at an age when they are growing comparatively slowly. This is probably the reason why his correlations

of weight at different ages did not allow Axelsson (1933) to support the suggestion of Bengtsson (1929) that the growth rates of a pig, before and after 20 kg. in weight, were independent. Berge (1936) observed a small correlation of $+0.139 \pm 0.040$ between the two rates, a result which, taken in conjunction with the present results, suggests that Bengtsson (also Dunlop, 1933) was substantially correct. Regarded in this light, the correlation between weaning weight and subsequent performance as usually computed, becomes a measure of the extent to which pre-weaning environment (principally milk production in relation to sow and nipple) affects age at slaughter weight. Such a correlation may be justifiably used for deductions concerning the environment of young pigs but not the pigs themselves. Under certain conditions, some modification of this interpretation requires to be made. If the assumption cannot be made that light pigs incur no permanent injury to their powers of growing, then some degree of correlation between weaning weight and subsequent growth calculated in either fashion is to be expected. In general, the numbers of such pigs in herds with weaning weights averaging 30 lb. or more will be rather few.

SUMMARY

1. The post-weaning growth of 135 litters has been analysed with a view to determining the relationship of certain arbitrary subdivisions with each other. For this purpose, the weight increases during three periods of 28 days have been defined in two ways—first, by age, the periods being 10–14, 14–18, and 18–22 weeks, and secondly, by weight, the periods beginning at 40, 80 and 120 lb. and continuing as before for 4 weeks.

2. When the periods are defined by age, the mean increase per pig per litter is affected by weaning weight, but not by litter size (Table III). The variability of the individual increases becomes greater as the pigs become older and heavier (that is, passing from one period to a later one), but less within a period as the rate of growth increases (Table IV). It was not affected by litter size.

3. The distribution of individual weights became increasingly skew with age. This is regarded as a graphical illustration of the fact that while absolute rate of growth is increasing, initially small animals must fall farther and farther behind (Graph 3).

4. The correlations between the average litter increases in different periods were calculated for litter sizes 6–11. In general, the coefficient

for periods 1 and 2 was about 0.4, and for periods 2 and 3 about 0.6 (Table VI). This is interpreted to mean that, when judged by results over the whole time under observation, litters with a high correlation between the increases in weight during short periods are not properly comparable with those with a low correlation. By this method, differences in rate of growth having an important influence on carcass quality may be obscured.

5. Since the correlations of the total increase during all three periods with those during the second and third periods were scarcely affected by removing the effect of the increase in period 1, it is concluded that, under Shothed conditions, the weights of the pigs at 10 weeks are too low to ensure that post-weaning checks are avoided. A more reliable test would be obtained by considering only the growth from the second period onwards, that is, from 14 weeks old.

6. When the periods are defined by weight, differences between litters in amount of weight put on in 28 days are still significant in each of the three periods (Table VII). Differences in weaning weight were more marked than the differences in subsequent growth.

7. No effect of weaning weight on subsequent growth during the periods defined by initial weight was observed.

8. The correlation between the average litter-increases for the second and third periods was 0.47 for litters of eight and 0.44 for litters of nine. The corresponding figures for the periods defined by age were 0.50 and 0.50. These comparatively low correlations suggest that careful control of environment in testing stations is necessary for reliable litter testing, and that results from such stations should be examined for evidence of genetic differences in rate of growth during restricted portions of the total test period.

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THE QUANTITATIVE EXTRACTION OF CAROTENE FROM GRASS

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NUMEROUS methods have been devised for the separation of carotene from grass and other green vegetable material, and most of these involve a preliminary extraction of total carotenoids followed by a phase separation to obtain the carotene-xanthophyll ratio. The usefulness of such methods is restricted by the limitations of the phase separation. This process necessitates removal of the carotenoid solvent in an inert atmosphere, followed by a partition between petroleum ether and methyl alcohol, a procedure which is not particularly well adapted for rapid routine work and the simultaneous analysis of several samples. Moreover, in order to obtain the carotene content of a single sample three individual determinations are usually required, viz. (1) total carotenoids, (2) carotene fraction in the phase separation, and (3) xanthophyll fraction in the phase separation. This is hardly conducive to accuracy in the resulting figure for carotene content.

In order to dispense with the phase separation a direct extraction of carotene, immediately after the saponification of chlorophyll and without a preliminary determination of total carotenoids, is much to be desired. Direct extraction with petroleum ether presents an obvious means of achieving such a result, and has in fact been suggested by Ijdo (1936), as a modification of the method of Guilbert (1934). Experience has shown that to avoid the formation of emulsions in the extraction of alkaline saponates with petroleum ether, the presence of alcohol is essential. Guilbert's method of analysis employs initial saponification with alcoholic potash, instead of the more usual aqueous potash, and is therefore easily adaptable to extraction with petroleum ether. The use of hot alcoholic potash for the disintegration of leaf material and saponification of chlorophyll is, however, subject to one very serious disadvantage. Alkaline extracts of grass contain resinous substances which are precipitated in the presence of alcohol. This brown or red precipitate is of rather uncertain nature, probably derived largely from mucilage and hemicellulose materials, and is thrown down in close contact with the substance being analysed. Subsequent extraction with

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solvents is rendered very difficult, especially in the case of finely ground grass meals. In order to overcome this difficulty it is necessary to treat with alcohol and potash separately. There are thus two alternatives:

(1) Extraction of the grass with hot alcohol, followed by treatment of the extract with potash.

(2) Saponification with hot aqueous potash, followed by filtration and extraction of the grass residue with alcohol.

The first of these methods has been employed by a number of workers, notably Deleano & Dick (1933), De (1936) and Wilson *et al.* (1937), all of whom employ a preliminary mechanical breakdown of the plant material, with sand or powdered glass. In most cases a second solvent, such as petroleum ether or acetone, has been considered necessary to complete the extraction. All these methods require thorough pulverization of the leaf tissue,¹ to permit complete extraction of pigments. In the author's experience disintegration by grinding with powdered glass has not been found very suitable for grass, a coarser material, such as sand, being far superior; even the latter, however, cannot be regarded as entirely satisfactory. Furthermore, samples of milled dried grass have proved to be more difficult to extract by these methods than fresh green leaves.

An examination of numerous methods of analysis has indicated that some process of mechanical breakdown is a very necessary preliminary to pigment extraction with solvents. Grinding is laborious and it is difficult to achieve efficient breakdown of plant cells by this means. On the other hand, saponification with potash is a simple and convenient process for the disintegration of cellular tissue under standardized conditions, and facilitates the removal of chlorophyll. Furthermore, for a wide range of fodder materials—straw, hay, silage, fresh and dried grass, etc.—potash saponification methods appear to be of much greater general utility than direct extraction with solvents.

The advantages associated with a preliminary saponification process have led to the adoption of the second method outlined above for the extraction of carotene from grass and other fodder materials. Details of this method are given below.

¹ More recently, Bolin & Khalapur (1938) have adopted alcohol extraction without any previous mechanical disintegration process and without the use of any other solvent. This seems less likely to result in complete removal of carotene, but a preliminary examination of the method has shown that the amount of carotene remaining after extraction may be quite small; further experience is necessary to indicate the usefulness of this process for materials other than dried grass meal. It should be pointed out that oxidation—due to heat treatment in the absence of stabilizing alkali—may possibly occur under the conditions of this method.

METHOD

5 g. of finely chopped fresh grass or 2 g. of dried grass meal are boiled for $1\frac{1}{2}$ hr. with 40 c.c. 20% potassium hydroxide in an Erlenmeyer flask fitted with reflux condenser.

After cooling, the contents of the flask are filtered under reduced pressure through moistened cotton-wool, supported on a perforated porcelain disk. The residue is transferred to a beaker, washed four times with 25 c.c. portions of ethyl alcohol (industrial spirit), and then with petroleum ether until this remains colour-free. The fourth alcohol solution rarely contains much colour and a single treatment with petroleum ether usually suffices to complete the extraction of carotene. All alcoholic and petroleum washings are poured through the filter. The grass residue remains coloured green owing to the presence of potassium isochlorophyllin, which is only slightly soluble in organic solvents but readily dissolves in water.

During this stage precipitation occurs in the filter flask owing to the reaction between alkaline and alcoholic extracts. This is completed by shaking, after which the precipitate is filtered off under reduced pressure, and washed with petroleum ether.

The combined alcohol and petroleum ether extracts are now transferred to a separating funnel and well shaken; after separating the two layers the alcohol fraction is extracted three more times with fresh petroleum ether. The colour contained in the final petroleum ether extract should be entirely removed by 92% methyl alcohol, indicating that the extraction of carotene is complete. If any colour remains on testing with 92% methyl alcohol, further extraction of the original alcohol layer with petroleum ether is necessary.

When all the carotene has been thus removed the combined petroleum ether solutions are shaken repeatedly with 92% methyl alcohol until this remains colour-free. The resulting solution of carotene in petroleum ether is washed with distilled water, and the quantity of pigment present may then be determined by colorimetric or other means.

RESULTS

Determinations of the carotene in several hundred samples of fresh grass and in numerous dried grasses have been carried out by this method during 1938. The process described has proved to be much shorter than those involving a separation of total carotenoids, and the results obtained may be reproduced with considerable accuracy.

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In order to obtain the standard error for carotene extraction by this method, ten replicated determinations were made on a single sample of dried grass meal, using the Lovibund tintometer and Ferguson's (1935) carotene curve for colorimetric evaluation of the extracted pigment. A comparison was also made with results obtained by the methods of Ferguson & Bishop (1936) and Pyke (1936), the former being representative of the "total carotenoid extraction" methods, and the latter a rapid process which has attracted some considerable attention since its recent introduction. The results obtained are shown in Table I, quantities of pigments being expressed as mg. per 100 g.

Table I

Method	Moon	Ferguson & Bishop			Pyke		
		Total carotenoids	Carotene Xanthophyll	Carotene	Carotene	Xanthophyll	Carotene Xanthophyll
Fraction	Carotene						
	22.81	98.13	0.372	26.61	24.84	12.32	2.017
	22.67	94.28	0.402	27.04	23.10	11.11	2.079
	20.98	91.52	0.384	25.39	25.41	15.79	1.609
	22.65	90.61	0.411	26.38	28.35	13.53	2.095
	21.52	88.41	0.366	23.69	28.25	16.48	.714
	23.11	85.45	0.370	23.09	30.09	16.70	.802
	23.44	88.18	0.369	23.77	26.88	15.66	.716
	23.36	87.46	0.327	21.55	28.28	7.88	3.588
	23.25	86.24	0.353	22.50	20.70	13.66	.516
	23.66	89.23	0.401	25.54	25.96	15.13	.716
Mean	22.75	89.95	0.376	24.56	26.19	13.83	1.985
Standard error:							
Actual	0.86	3.87	0.025	1.89	2.81	8.33	1.79
Percentage of mean	3.78	4.30	6.65	7.70	10.73	60.23	90.18
Standard error of mean:							
Actual	0.27	1.22	0.008	0.60	0.89	2.63	0.57
Percentage of mean	1.19	1.36	2.13	2.44	3.40	19.02	28.72

It is evident from these figures that the standard error of the method under examination compares favourably with those for determinations according to Ferguson & Bishop or Pyke. Furthermore, it appears that the latter method is of little or no value for the determination of xanthophyll or of carotene-xanthophyll ratios. An examination of the influence of strength of methyl alcohol on the carotene-xanthophyll ratio (Moon, 1938) has revealed that a concentration of at least 90% (by vol.) is necessary for complete extraction of xanthophyll; lower concentrations, such as the 85% used in Pyke's method, failing to completely extract the xanthophyll, lead to a low figure for this pigment and a

correspondingly high value for carotene. By using 92% methyl alcohol in Pyke's method, mean carotene and xanthophyll contents of 14.98 ± 1.20 and 41.01 ± 4.16 , respectively, have been obtained for the same sample of dried grass, the carotene-xanthophyll ratio being 0.368 ± 0.0087 . It must be concluded that when Pyke's procedure is adopted, the extraction of both carotene and xanthophyll is incomplete, the inefficient separation of the two carotenoids leading to a very low figure for xanthophyll, and a carotene value which is somewhat similar to that obtained by other methods.

The *t* test has been applied to the three mean carotene figures in Table I, in order to examine the significance of their differences. It appears from the results of this test, summarized in Table II, that the

Table II

	Difference between means	Standard error	<i>t</i>	<i>P</i>
Moon <i>v.</i> Ferguson & Bishop	1.81	0.657	2.755	<0.02
Moon <i>v.</i> Pyke	3.44	0.930	3.699	<0.01
Pyke <i>v.</i> Ferguson & Bishop	1.63	1.071	1.522	>0.10

amount of carotene extracted by the method described above differs significantly from the amounts obtained by the other two procedures, although the difference between these other two methods is not significant.

Since it is possible for differences in variance to contribute to a significant value of *t*, the three variances have been separately estimated

Table III

	Degrees of freedom	Sum of squares	Mean square	$\frac{1}{2} \log_e$ mean square
Moon	9	6.723	0.747	1.0054
Ferguson & Bishop	9	32.161	3.573	1.7881
Pyke	9	71.136	7.904	2.1844
		<i>z</i>	<i>P</i>	
Moon <i>v.</i> Ferguson & Bishop		0.7827	<0.05	
Moon <i>v.</i> Pyke		1.1790	<0.01	
Pyke <i>v.</i> Ferguson & Bishop		0.3963	>0.05	

and the significance of their differences tested by the *z* method. From the analysis of variance in Table III it is clear that the value of *z* is significant in two cases, viz. Moon *v.* Pyke and Moon *v.* Ferguson & Bishop.

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The results of the *z* test do not justify the conclusions drawn from Table II, and no significance can therefore be attached to the difference of 7.6% in the mean results for Moon *v.* Ferguson & Bishop. Even if significant, however, such a difference could not be considered a sufficient reason for rejecting the new method, which yielded the lower result. Thus the two carotenoids are not of equal colour intensity (Willstätter & Stoll, 1913), and the use of a "carotene" curve to determine both pigments may possibly lead to an overestimation of carotene in methods of the Ferguson & Bishop type (Moon, 1938).

As Table III clearly indicates that the results obtained by the new method are subject to much less variation than those of the other two, it must be concluded that this process is superior for the quantitative extraction of carotene from grass. Indeed, the small variance and standard error make it doubtful whether any greater accuracy could be obtained using the same colorimetric evaluation of the extracted pigment.

SUMMARY

The majority of methods for determining carotene involve a preliminary determination of total carotenoids, followed by a phase separation of the two pigments. This phase separation considerably limits the usefulness of such methods, and in order to dispense with it a direct extraction of carotene is necessary. For this purpose petroleum ether may be used in the presence of alcohol.

The use of hot alcoholic potash for the disintegration of leaf material and separation of chlorophyll leads to a very undesirable precipitate which hinders subsequent extraction. Two alternative methods are available, which overcome this difficulty, viz. (1) extraction with hot alcohol, followed by treatment of the extract with potash, and (2) saponification with hot aqueous potash, followed by filtration and extraction of the grass residue with alcohol. The second of these methods has been adopted, being of greater general utility and capable of producing complete cellular breakdown, which is essential for efficient extraction. Details of this extraction process have been described.

A comparison of the results obtained, with those from two other methods, has been made by a colorimetric determination of the extracted pigment. The variance and standard error have been shown to be smaller than those for the other two methods, and it has been concluded that the results obtained are reproducible with considerable accuracy.

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NOTE ON THE EFFECT OF TEMPERATURE ON A MIXED CULTURE OF TWO ORGANISMS IN SYMBIOTIC RELATION

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(With One Text-figure)

IN view of the interest recently taken in the behaviour of microbes in mixed culture (Nicol, 1934; Waksman *et al.* 1937; Vaughn, 1938), it has seemed desirable to publish some observations made so long ago as 1917 as an outcome of work on the fixation of nitrogen in faeces (Richards, 1917). It was then shown that in the early stages of fermentation of manure, fixation of nitrogen can occur under certain conditions. The faecal matter is the principal source of energy for the organisms concerned, but the straw also contributes in some degree to the increase of nitrogen. Hence study of the relation of nitrogen-fixing bacteria to carbohydrate material is necessary.

In attempting to isolate the nitrogen-fixing organisms from the fermenting manure, two species were found frequently on dextrose-agar plates; both grew well in mixed culture in presence of chalk in liquid dextrose and liquid starch media, especially the latter. The two organisms were a strain of *Azotobacter chroococcum*, and a capsuled organism of the *Aerogenes* type.

The morphological and cultural characters of these organisms were outlined by Richards (1917).

To find their optimum temperatures, the two organisms were grown separately and in combination at temperatures of 20, 25, 30 and 35° C. In 2% dextrose, a pure culture of *Azotobacter* fixed nitrogen as is shown in the lowermost two curves of Fig. 1. The optimum temperature for *Azotobacter* was therefore somewhere between 25 and 30° C., say 28° C.

With the *Aerogenes* organism, the gas production in dextrose broth was measured in calibrated Durham fermentation tubes.

The results are given in Table I.

Table I

Ml. of gas in tube after	at ...20° C.	25° C.	30° C.	35° C.
24 hr.	0.00	0.01	0.17	0.34
48 hr.	0.00	0.14	1.14	1.50 (full)
72 hr.	0.08	0.35	1.35 (full)	1.50 (full)

These figures are, of course, merely comparative, but they show that the activity of the *Aerogenes* organism increases rapidly with rise of temperature from 20 to 35° C.; i.e. the organism behaves quite normally as a member of the *coli* group, and therefore has its optimum close to 37° C., about 10° higher than the optimum for *Azotobacter*.

The mixed culture of *Azotobacter* and *Aerogenes* was tested for nitrogen-fixation at four temperatures in 2% starch phosphate. Growth in this medium was good at all temperatures, as shown by clarification of

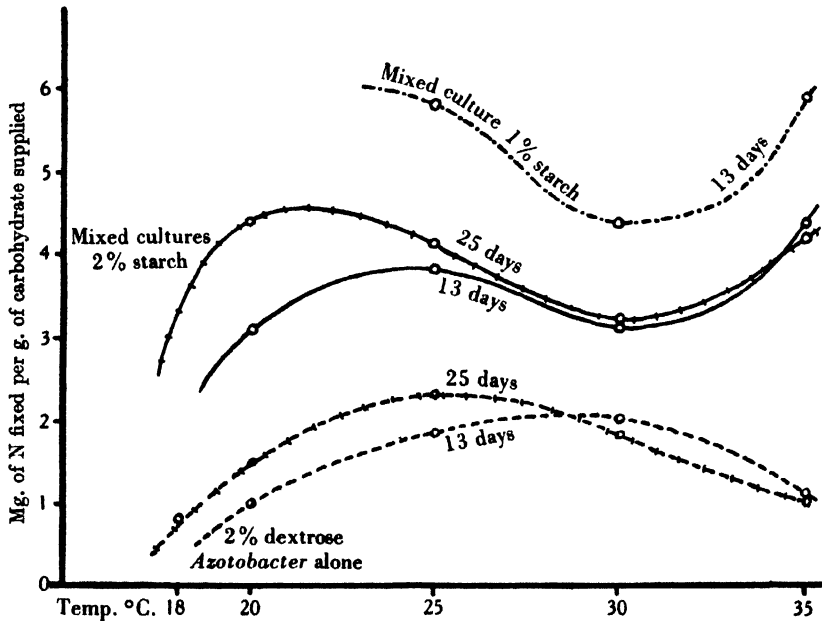


Fig. 1.

the starch and formation of a strong white scum, turning brown in old cultures.

After 4 or 5 days' incubation, alcohol was produced in such quantity in the cultures incubated at 25° C. and over that it could be smelt without removing the plugs.

As it is known that nitrogen-fixing organisms utilize carbohydrate more economically when it is presented to them in low concentrations, the action of the mixed culture was tried at three temperatures on 1% starch; in the result, the fixation of nitrogen per gram of carbohydrate supplied was much increased over the amounts found when 2% starch was given.

The results of all these tests are shown in the uppermost three curves of Fig. 1.

In all three series the fixation of nitrogen at 30° C. was less than 25 or 35° C. This double optimum temperature is peculiar, and seems worth following up.

The contrast in the course of nitrogen-fixation in pure culture and in a mixed culture can be easily seen from the figures. Theoretical consideration suggests a possible explanation of the lesser nitrogen-fixation at 30° C. *Azotobacter* seems to be unable to utilize starch directly for nitrogen assimilation, but requires that it shall first be converted into the simpler five- or six-carbon sugars or alcohols. *B. lactis aerogenes* and probably other members of the *Aerogenes* group are known to produce amylase and other enzymes. The action of these on the starch supplies the *Azotobacter* with the sugar necessary for its development.

The double maximum of nitrogen-fixation in mixed cultures leads to the following suppositions concerning them:

At temperatures about 20° C. *Azotobacter*, though not quite at its pure-culture optimum, is fixing nitrogen very efficiently, being supplied with only small amounts of carbohydrate made available for it by the hydrolysing activities of the *Aerogenes* organism. At about 35° C. the *Aerogenes* organism is working rapidly and is making relatively large quantities of carbohydrate available, but as 35° C. is above the optimal temperature for *Azotobacter*, the latter organism is not able to make efficient use of the carbohydrate at its disposal. *Azotobacter* at 35° C. is therefore acting inefficiently, and only the generous supply of available carbohydrate enables it to fix a notable total quantity of nitrogen. At intermediate temperatures such as 30° C., and at temperatures below 20° C., a low efficiency of nitrogen-fixation is coupled with a less than maximal amount of available carbohydrate, or else a fairly high efficiency in nitrogen-fixation cannot, for want of an adequate carbohydrate supply, lead to a notable total of fixed nitrogen.

These considerations assume, of course, that the properties of the organisms in mixed culture are similar to those of each of the organisms alone. In other words, the assumption takes no account of any interplay which the mixed organisms may have on each other. Such interplay may in some cases of association be important, but there is no evidence of it in the present results, nor does it seem necessary to assume any.

It should be borne in mind, however, that the curves are integrals, not rates.

There remains the question of toxicity. The anaerobic fermentation of glucose by *B. lactis aerogenes* has been very carefully studied by Harden

& Walpole (1906), who found ethyl alcohol and acetic acid among the products of its action. Either of these substances, if present in quantity, will inhibit the assimilation of nitrogen by *Azotobacter*. The chalk added to all the cultures will tend to keep the reaction neutral, but at the surface of the medium where the *Azotobacter* develops most freely, the acidity may still be appreciable.

Is it reasonable to assume that the proportional distribution of the products of enzyme action under the conditions of the present experiments may be influenced by temperature, so that more alcohol accumulates at one temperature and more acid at another? At 25° C., *Azotobacter* is near its optimum, while *Aerogenes* may not be sufficiently active to exert much inhibitory action; at 30° C., *Azotobacter* is not at its best, but *Aerogenes* is very near its optimum. At 35° C., alcohol may not be formed as readily as at 30° C., or its concentration may be less, owing to increased volatilization at the higher temperature. Also, as *Aerogenes* itself is able to fix small amounts of nitrogen (0.3 mg./g. of carbohydrate at 25° C.), its vigorous growth at temperatures near its optimum will increase further the total nitrogen found.

This discussion instances the complications that ensue upon mixture of organisms. The full study of even two organisms when growing together presents many difficulties, but in these difficulties lies the fascination of such problems.

SUMMARY

1. A study was made of nitrogen-fixation by *Azotobacter chroococcum* alone in a medium containing dextrose (which it can utilize) and in mixture with a coliform organism on a medium containing no carbohydrate except starch, which *Azotobacter* cannot utilize unless it be hydrolysed by the coliform organism or some other agency.

2. The amount of nitrogen fixed in the mixed cultures was found to be maximal at two temperatures, and a discussion is given of the causes thought to be operative in producing the double maximum.

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THE BASE STATUS OF SCOTTISH SOILS

II. FURTHER STUDIES OF THE EFFECTS OF LIME ON TYPICAL SOILS FROM NORTH-EAST SCOTLAND

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(With Four Text-figures)

In Part I of this investigation Mitchell (1936) reported field and laboratory experiments carried out to study the effects of lime, during the twelve months after its application, on five typical soils derived from different geological formations in the north-east of Scotland. It was found that the liming factor of the soil on olivine norite was much lower than the others, a greater percentage of the added lime entering the exchange complex.

In the present paper the following points are studied:

- (1) The effects of lime on the base status of these soils during the second and third years after application.
- (2) The movement of the lime into the subsoil.
- (3) The extension of the investigation to two additional soils; one derived from slate and the other from olivine norite.
- (4) Physical investigations on the soils and their clay fractions.

1. THE EFFECTS OF LIME ON THE BASE STATUS DURING THE SECOND AND THIRD YEARS

Five soils were treated in March 1932 with slaked lime at rates equivalent to 1 ton and 2 tons CaO per acre. Each treatment was replicated six times. Representative samples of surface soil were taken to a depth of 9 in. at six-monthly intervals. Chemical analyses and pH determinations were made using the methods employed by Mitchell (1936).

The location of the soils and the physical and chemical analyses will be found in Mitchell's paper (1936). Throughout the present text the soils will be referred to by the farm names: Overhill till from basic and acidic rocks; Drumnagair till from old red sandstone; Inschfield glacial drift from olivine norite; Danestone till from granite and gneiss; Craigiebuckler till from granite and gneiss.

Experimental results

The most important point emerging from the further investigation is that only slight changes have taken place in the base status of four of the soils during the second and third years, and there has been very little falling away from the maximum response to liming. On the fifth soil, Drumnagair, the effect of the lime shows a marked decrease early in the investigation particularly on the lightly limed plots.

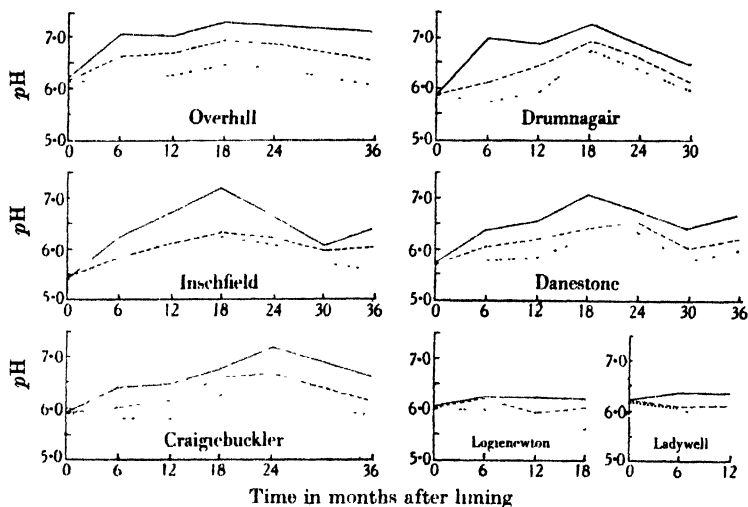


Fig. 1. *pH* determinations on surface samples (moist soils in aqueous suspension).

— 2 tons - - 1 ton 0 ton

(a) *pH determinations.* The *pH* values of the limed and unlimed moist soils will be found in Fig. 1. For the sake of continuity the results obtained by Mitchell for the surface samples have been included. Considerable variation in the unlimed plots at the different times of sampling can be noted, the maximum variation over the 3-year period being 1.0 *pH* unit at Drumnagair and the minimum 0.3 at Overhill. At Overhill and Craigiebuckler the maximum response, as shown by the *pH* values, appears to have been reached a considerable time after liming. This is to some extent supported by the percentage saturation figures. The two granitic soils show a general similarity in response over the period. The final samplings give the same value for the two centres, an increase of about 0.4 *pH* unit on the 1-ton plots and 0.7 on the 2-ton. The greatest response at the final sampling, 1.1 *pH* unit, is shown by the 2-ton plots at Overhill. The falling off in the effect at Drumnagair is shown markedly

on the 1-ton plots, where the increase in *pH* over that of the unlimed plots is 0.5 12 months after application and only 0.15 at the end of 30 months. On the more heavily limed plots this drop in response is not so marked—from 1.0 at the end of 12 months to 0.5 at the end of 30 months. This reacidification relative to the unlimed plots had taken place before the 18-month sampling, and during the following year there was practically no change. Generally the increase in *pH* caused by the application of 2 tons of lime is about twice as great as that due to 1 ton, and this relationship obtains throughout the period.

(b) *Exchangeable calcium and percentage saturation.* The exchangeable calcium figures are given in Table I. Estimations were also made of exchangeable magnesium, sodium and potassium. Exchangeable hydrogen was determined by Parker's method of leaching with barium acetate and titrating the leachate. The calcium figures for the untreated plots show considerable variation from sampling to sampling, but no definite seasonal trend. This variation is probably to be associated with ordinary sampling errors. At the 30-month sampling four of the soils show similarity in the exchangeable calcium content, about 10 m.e. on the 2-ton plots, 8 m.e. on the 1-ton and 6 m.e. on the unlimed. Drumnagair alone returns low values, 7.4, 6.6 and 5.8 m.e. for the different treatments. In a study of the effect of lime on the base status consideration should also be given to the exchangeable hydrogen. Whilst the calcium of the unlimed soil has the relatively narrow range of from 5.1 m.e. at Drumnagair to 9.8 m.e. at Craigiebuckler (as the extreme values of individual samplings), the hydrogen varies from 3.4 m.e. at Drumnagair to 15.2 m.e. at Inshfield.

A more useful indication of the base status is given by the degree of saturation, that is, the sum of the basic cations expressed as a percentage of the total cations (Fig. 2). The two soils with the lowest base exchange capacity, i.e. Overhill and Drumnagair, are the most saturated, whilst the soils with greater exchange capacity are much less saturated. Of the two soils at a high saturation level, one—Overhill—maintains that level for approximately 3 years after liming, whilst at Drumnagair there is a decline after 1 year. This difference in behaviour is apparent also from the *pH* values given in Fig. 1 and is possibly to be associated with the relatively low base-exchange capacity of Drumnagair. An approximate value for carbonate content was obtained by means of the Collins calcimeter. Twelve months after liming small amounts of carbonate could be detected in all the heavily limed soils except those at Drumnagair.

Mitchell's results show an increase in exchangeable magnesium of limed over unlimed plots 1 year after application, but at the time of the last sampling this difference had almost disappeared. The only soil with a greater magnesium content in the limed plots is Overhill, a soil with a high initial content of exchangeable magnesium. At Inchfield, where

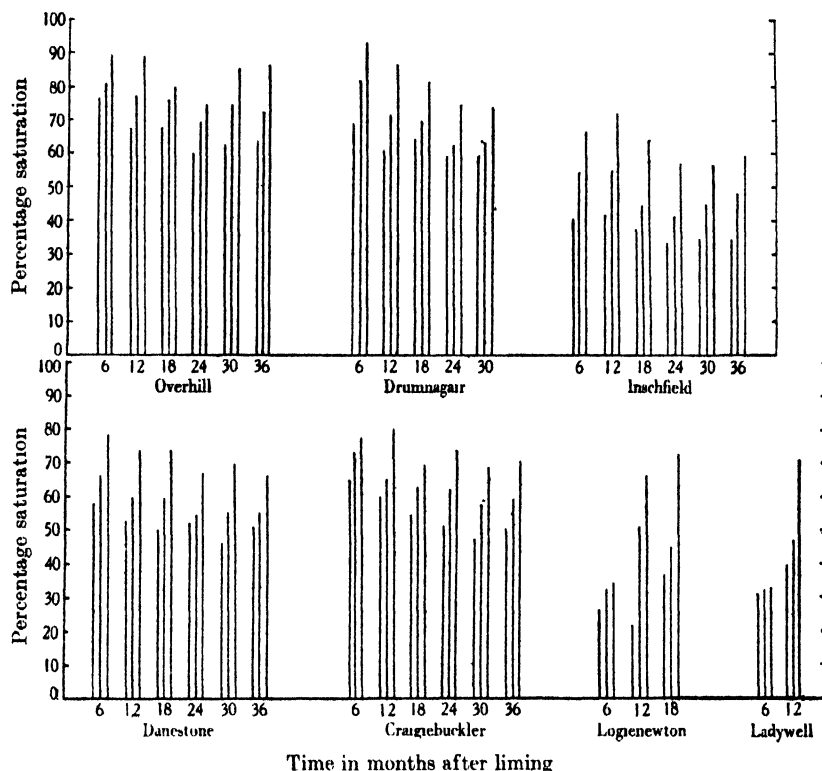


Fig. 2. Percentage saturation figures for surface samples. In each set of three figures, the left-hand one refers to the unlimed plots, the centre to the 1-ton and the right hand to the 2-ton dressing.

the percentage utilization of the added lime is high (p. 313) and the magnesium content low, the ratios of calcium to magnesium 3 years after application are 5.7 on the unlimed, 9.3 on the 1-ton and 11.3 on the 2-ton plots: at Overhill, where the percentage utilization is low and the magnesium content high, the corresponding ratios are 2.6, 3.1 and 3.6. Only slight variations were noted in sodium and potassium following liming, and these did not show any definite trend.

2. THE MOVEMENT OF THE LIME INTO THE SUBSOIL

Stewart & Wyatt (1919) found that limestone applied to surface soil had some effect in neutralizing subsurface acidity, but the process was very slow. Wilson (1930) noted similar results when CaCO_3 was applied to soil in cylinders, but found that the adsorption did not extend below 2 ft. The subsurface samples in the present investigation were taken at a depth of 9–18 in., and at 18, 24, 30 and 36 months after application of lime. The average pH values of the unlimed subsurface soils are Overhill

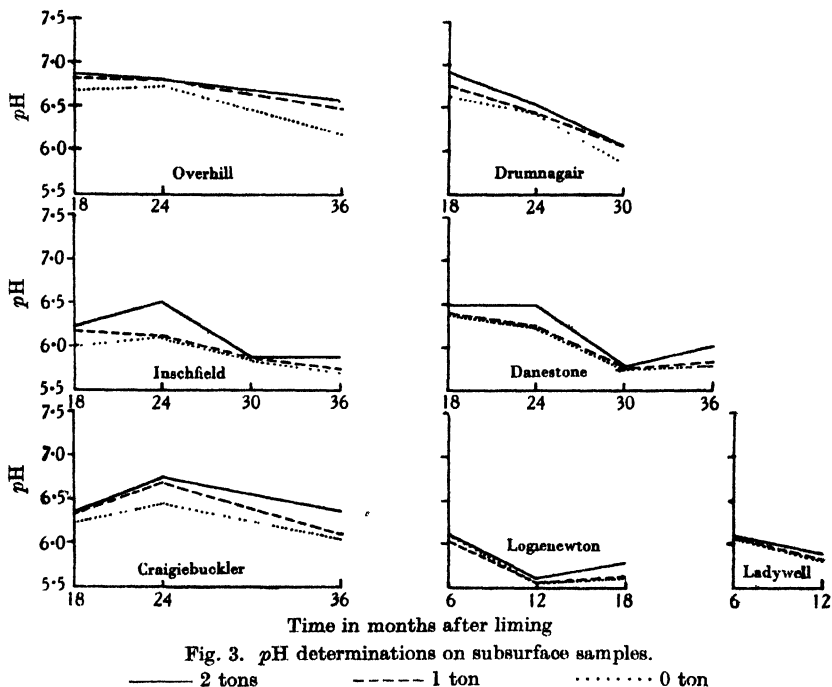


Fig. 3. pH determinations on subsurface samples.

— 2 tons - - - 1 ton 0 ton

6.5, Drumnagair 6.4, Inshfield 5.9, Danestone 6.0 and Craigiebuckler 6.3. The changes in pH due to liming are shown in Fig. 3, where the values are graphed at 18, 24, 30 and 36 month samplings. There does not appear to be any definite seasonal trend or any marked falling away in response during the time of the investigation. Application of 1 ton appears to have only a very slight effect on the subsurface soil. On the 2-ton plots the five soils show similar results, an average of about 0.2 pH unit increase over the period.

The figures for exchangeable calcium are given in Table I. Drumnagair and Inshfield show no increase due to liming. The other three

Table I. *Exchangeable calcium in soils receiving 0, 1 and 2 tons CaO respectively (as m.e. per 100 g. air-dry soil)*

	Months since liming	Overhill			Drumnagair			Inschfield			Danestone			Craigiebuckler		
		0	1	2	0	1	2	0	1	2	0	1	2	0	1	2
Surface	18	6.8	8.7	9.7	5.3	6.1	8.6	6.0	8.3	12.5	6.6	7.2	10.4	8.7	10.6	12.3
	24	5.8	7.3	8.5	5.5	6.5	7.8	5.5	7.8	11.6	6.7	7.2	9.7	7.9	9.7	12.2
	30	6.4	8.2	9.6	5.8	6.6	7.4	5.1	7.7	11.6	6.2	6.9	10.1	7.0	9.1	11.1
	36	7.3	8.6	11.2	—	—	—	6.4	9.1	12.7	7.8	8.5	11.2	8.6	10.7	12.4
Subsurface	18	4.9	5.5	6.0	5.3	5.3	5.3	6.7	6.8	6.8	4.7	5.3	5.5	6.0	7.0	7.6
	24	5.3	5.8	6.0	5.6	5.7	5.8	6.1	5.8	5.8	5.2	6.0	6.2	7.0	8.2	8.6
	30	6.4	7.2	7.3	6.3	6.0	6.1	5.4	5.3	5.6	5.0	5.6	5.7	6.2	6.3	7.3
	36	6.6	7.2	7.3	—	—	—	5.7	5.7	5.9	5.2	5.3	6.2	7.8	8.0	9.0

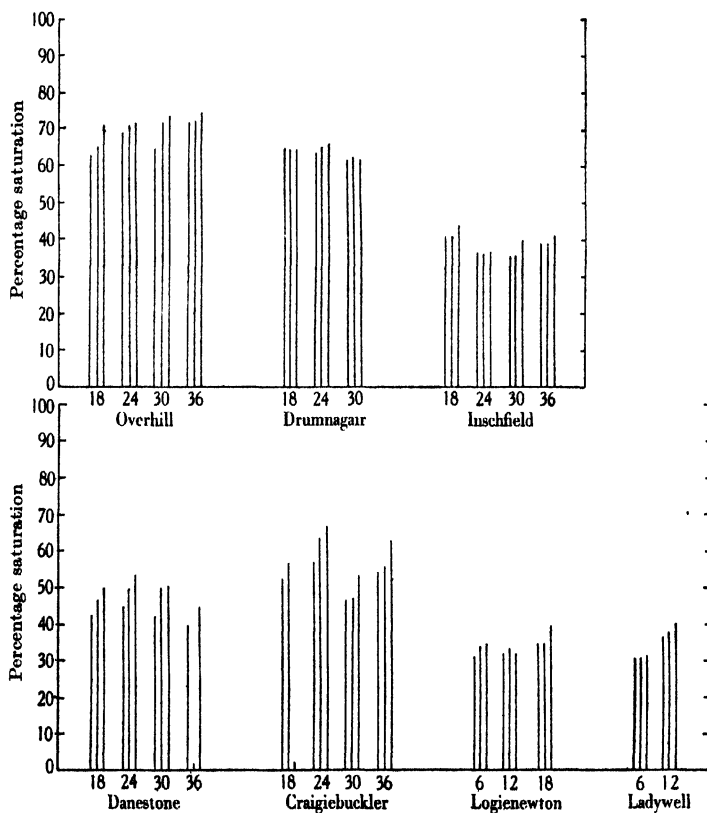


Fig. 4. Percentage saturation figures for subsurface samples. In each set of three figures, the left-hand one refers to the unlimed plots, the centre to the 1-ton and the right hand to the 2-ton dressing. One figure has been omitted at Danestone and one at Craigiebuckler owing to insufficient data.

soils show an increase over the unlimed plots of about 0.6 m.e. per 100 g. air-dry soil for the 1-ton dressing, and 1.0 m.e. for the 2-ton dressing. The effect on the base status will be seen from the percentage saturation results given in Fig. 4. Danestone, Craigiebuckler and Overhill show a slightly increased base saturation due to liming. Drumnagair and Inschfield show practically no change.

3. EXAMINATION OF ADDITIONAL SOILS

One of the most important points that resulted from the previous investigation was the relatively low liming factor of the Inschfield soil. To confirm this a similar series of plots was put down on a neighbouring farm. A second series was also undertaken on a soil derived from slate, a type new to the investigation. The general characteristics of these soils are given in Table II and the chemical and mechanical analyses in Table III.

Table II. *Characteristics of the additional soils*

Farm name and locality	Parent material	Surface 9 in.
Ladywell, Aberdeenshire	Thin glacial drift derived from local olivine norite rocks	Yellowish brown medium loam
Logienewton, Aberdeenshire	Slate boulder clay overlying slate	Brownish grey medium loam

Table III. *Analyses of additional soils*

Ultimate chemical analysis as percentage ignited soil			Mechanical analysis as percentage air-dry soil (< 2 mm.)		
	Ladywell	Logie-newton		Ladywell	Logie-newton
SiO ₂	52.64	69.58	Coarse sand	21.1	10.3
Fe ₂ O ₃	12.52	6.26	Fine sand	30.5	29.2
Al ₂ O ₃ etc.	23.83	18.95	Silt	15.2	27.4
CaO	4.62	0.91	Clay*	19.9	19.2
MgO	3.72	0.94	Air-dry moisture	7.7	5.8
Na ₂ O	2.01	1.95	Difference	5.6	8.1
K ₂ O	1.11	1.97		100.0	100.0
	100.45	100.56	Loss on ignition	12.1	12.4
pH of moist soils in aqueous suspension	6.02	5.73	Weight of 1 acre of soil (< 2 mm.) to 9 in. in million lb.	1.50	1.40
			* Including dissolved sesquioxides	2.3	1.6

The results for the Ladywell soil show a close similarity to those of the neighbouring soil at Inschfield (Mitchell, 1936). The basic nature of these soils is shown by the high contents of lime and magnesia. The Logienewton soil is characterized by a low lime and magnesia content, and by the relatively low proportion of coarse sand.

Experimental results

The most important point resulting from this part of the investigation is the low liming factor and the slowness of the response to liming.

(a) The pH increases due to liming (shown in Fig. 1) are on the whole similar to those noted by Mitchell. There is, however, a marked difference in the speed of the response. In the first series the maximum had been reached about 6 months after application, but in the second series the effect after 6 months was very slight. As a period of 18 months separated the two applications the difference in results may be associated to some extent with differences in climatic conditions.

(b) The changes in exchangeable calcium are given in Table IV. At the end of 6 months very little of the applied calcium has entered the exchange complex. At the end of 12 months there are increases in heavily limed over unlimed plots of 6.9 m.e. at Ladywell and 8.3 at Logienewton.

Table IV. *Exchangeable calcium in additional soils, m.e. per 100 g.*

	Ladywell						Logienewton					
	Surface			Subsurface			Surface			Subsurface		
Months since liming	Tons of lime			Tons of lime			Tons of lime			Tons of lime		
	0	1	2	0	1	2	0	1	2	0	1	2
6	4.5	4.8	4.8	3.5	3.3	3.7	4.2	5.3	5.5	4.1	4.4	4.3
12	6.1	7.9	13.0	3.5	3.9	4.5	4.3	8.1	12.6	4.0	4.3	4.2
18	—	—	—	—	—	—	6.1	8.7	14.2	3.7	3.9	4.6

At these two centres and at Inschfield about 80% of the applied lime is taken up by the exchange complex; at the other centres only about 50%. The lag in the neutralizing action of the lime at Ladywell and Logienewton can be seen from the percentage saturation values given in Fig. 2.

(c) *The liming factor.* The lime requirement was found by the neutralization curve method described by Mitchell (1936), and a comparison of the field result with that obtained in the laboratory for pH 6.0 in water gave the liming factor (Table V). The curves obtained resembled those given by Mitchell in his report. Ladywell was found to have a liming factor of 1.8 12 months after the application of lime. This figure is in fair agreement with that of 1.5 obtained by Mitchell at Inschfield. These two soils are of the same geological origin and are similar in chemical and mechanical composition. The factor for Logienewton was found to be 1.2. This soil is of different geological origin from the other two and differs also in chemical composition. A characteristic

common to the three soils is the relatively high clay content, about 19% of the air-dry (<2 mm.) soil, a value considerably higher than those of the other four soils.

Table V. *Base exchange capacity and exchangeable hydrogen in m.e. per 100 g. of the air-dry unlimed soils and their liming factors to pH 6.5*

	After 1 year (Mitchell's results)			After 3 years		
	Liming factor	Base exchange capacity	Exchangeable hydrogen	Liming factor	Base exchange capacity	Exchangeable hydrogen
Overhill	2.4	14.0	4.5	4.5	16.6	6.2
Drumnagair	3.0	10.5	4.1	5.5	12.0	4.8
Craigiebuckler	2.5	17.0	7.0	2.0	19.2	9.5
Danestone	3.1	15.6	7.5	2.7	17.1	8.3
Inschfield	1.5	21.4	12.4	1.8	23.1	15.2

To reach an aqueous pH of 6.0

	After 6 months			After 12 months			After 18 months		
	Liming factor	Base exchange capacity	Exchangeable hydrogen	Liming factor	Base exchange capacity	Exchangeable hydrogen	Liming factor	Base exchange capacity	Exchangeable hydrogen
Logienewton	5.3	21.4	15.7	1.8	19.2	13.2	1.2	20.6	13.0
Ladywell	10.0	20.1	14.0	1.8	19.1	11.5	—	—	—

The results given in Table V indicate that soils with a large content of exchangeable hydrogen hold added lime more effectively than those with little exchangeable hydrogen. The liming factors for the Overhill and Drumnagair soils three years after liming are about double the values at the end of one year. The Danestone, Craigiebuckler and Inschfield soils show only small changes in the liming factors between the two samplings.

4. PHYSICAL INVESTIGATIONS

An attempt was made to determine the effect of liming on certain physical properties.

(a) *Hygroscopicity.* The hygroscopicity of the soil at a definite humidity is assumed to give an indication of the amount of colloiddally active material, and this has an important bearing both on physical and chemical properties.

In this investigation a humidity level of 50% was used, as suggested by Puri *et al.* (1925) so as to reduce to a minimum any difference in water content resulting from variations in the relative humidity. The soils were passed through a 2 mm. sieve and allowed to reach equilibrium in a large desiccator containing sulphuric acid of the required concen-

tration. Table VI shows that the percentage of moisture, on an oven-dry basis, increases in the same order as the sum of the exchangeable cations, indicating a relationship between base exchange capacity and surface activity. The results for the liming factors also show a relationship with the hygroscopicity values, the three soils with low liming factors having a high moisture content. The clay content of Drumnagair as shown by mechanical analysis is greater than that of Danestone. Danestone has, however, the greater loss on ignition and the greater exchange capacity. The hygroscopicity values point to Danestone having the greater amount of fine material. Whilst the effects of organic matter must not be overlooked, there is the possibility that in those soils of similar clay content the difference in the content of very fine particles may be considerable. In further study of the liming factor useful information might be gained from an investigation of the particle distribution curves for the finer fractions.

(b) *Heat of wetting.* When a dry soil is wetted with water combination occurs between the soil and the water, and this is accompanied by a rise in temperature. The amount of this rise is often taken as a measure of the extent of the soil surface. Heat of wetting is considered to be influenced also by the chemical composition of the soil. Janert (1934*a, b*) claims that the heat of wetting of a soil is related to the heat of hydration of the adsorbed ions and is highest for sodium and potassium, lower for calcium and magnesium and lowest for hydrogen.

The method used in this investigation is that proposed by Janert (1931). The soil (<1 mm.) was dried at 110° C. and a weighed amount at room temperature added to 100 c.c. water in a Dewar flask also at room temperature. The heat of wetting was found for soils as sampled in the field and also for calcium and hydrogen soils prepared in the laboratory by leaching soil from the untreated plots with *N* CaCl₂ solution or 0.05 *N* HCl respectively. In both cases the soil was finally well washed with distilled water. The values obtained are given in Table VI.

The base exchange capacity of the unlimed soils has been calculated by means of the Janert (1934*b*) approximate formula, i.e. base exchange capacity in m.e. per 100 g. soil = 4.2 times the heat of wetting in calories per gram. For comparison, the exchange capacity found by summing the individual cations is included. There is considerable variation in the heat of wetting of the unlimed soils, varying from 2.3 cal./g. at Drumnagair to 5.9 at Inschfield. It will be seen that in general the order for increasing heat of wetting is the same as that for exchange capacity by

Table VI. *Heat of wetting of soils (calories per gram)
and base exchange capacity (m.e. per 100 g.)*

Soil	Months after liming	Heat of wetting					Exchange capacity of unlimed soil		Field samples				Hygro- scopicity values 0 ton
		Field samples		Prepared soils		Cal- culated	Sum- mation	% Nitrogen		% Carbon			
		0 ton	2 tons	Ca	H			0 ton	2 tons	0 ton	2 tons		
Drumnagair	18	2.4	2.4	—	—	—	—	0.17	0.20	2.07	2.08	—	
"	24	2.3	2.5	3.2	2.4	9.9	11.2	0.18	—	2.11	—	2.8	
Overhill	36	3.2	3.3	4.2	4.1	13.4	14.4	0.16	—	2.09	—	3.5	
Danestone	36	3.1	3.0	3.4	2.8	12.6	16.0	0.32	—	3.71	—	3.9	
Craigiebuckler	18	4.0	4.4	—	—	16.2	17.8	0.28	0.30	3.70	3.61	4.0	
"	36	3.7	3.9	4.5	4.0	—	—	—	—	—	—	—	
Logienewton	12	4.1	4.8	—	—	—	—	—	—	—	—	—	
"	18	4.2	4.6	5.7	4.5	17.4	19.9	0.34	—	4.21	—	5.7	
Ladywell	12	4.2	5.4	7.2	6.0	17.6	19.7	0.35	—	4.13	—	6.9	
Inschfield	18	5.6	6.3	—	—	—	—	0.38	—	4.56	—	—	
"	36	5.9	6.1	7.4	6.0	24.2	20.9	0.40	0.38	4.48	4.49	7.6	

summation. This is in agreement with the findings of Janert and appears to indicate that the heat of wetting like the base exchange capacity is governed by some more fundamental property, such as the surface area.

Danestone with a clay content of only 10.7% as against 15% at Drumnagair has, however, the greater heat of wetting and the greater exchange capacity. The heat of wetting gives a somewhat closer correlation with the nitrogen content and the carbon content than it does with the clay content, indicating that it is with the total fine material of the soil, organic and inorganic, that the heat of wetting is to be associated. Generally the heat of wetting of the limed soil is somewhat greater than that of the unlimed. This increase is greatest for those soils with the greatest exchange capacity, indicating the importance of the nature of the adsorbed ion on the extent of the heat of wetting.

Turning to the hydrogen and calcium soils prepared in the laboratory it will be seen that the tendency is for the former to give values similar to those of the untreated field soils, whilst the latter give considerably higher results. This is in agreement with the findings of Pate (1925), who noted that a calcium-saturated soil has a higher heat of wetting than the corresponding hydrogen saturated soil.

In further work it would be desirable to measure the loss of humose material due to leaching in the laboratory and the alteration in the base-exchange capacity of the soil so caused.

The clay fraction

Samples of clay were prepared by a modification of the method used in mechanical analysis. Preliminary oxidation of the organic matter with hydrogen peroxide was omitted as were also the acid and the ammonia treatments. A portion of each clay sample was then boiled with hydrogen peroxide followed by thorough washing with water. Calcium clays and hydrogen clays were prepared from both the treated and untreated fine material, i.e. the clay with organic matter and the clay minus organic matter. The results are given in Table VII which also includes the $\text{SiO}_2/\text{R}_2\text{O}_3$ ratios of the clays.

Table VII. *Heat of wetting (calories per gram)
and $\text{SiO}_2/\text{R}_2\text{O}_3$ ratios of clays*

	Heat of wetting						
	Including organic matter			Minus organic matter			
Clay	Untreated	Ca	H	Untreated	Ca	H	SiO ₂ /R ₂ O ₃
Inschfield	13.7	13.5	11.6	9.7	10.2	10.4	1.51
Ladywell	13.6	12.3	11.1	9.2	8.4	8.7	1.51
Logienewton	7.4	7.8	7.1	4.7	5.0	4.6	1.93
Danestone	12.6	12.9	9.9	5.9	5.7	6.0	2.05
Craigiebuckler	11.0	9.2	6.2	4.5	4.4	4.0	2.11
Overhill	12.6	8.5	6.9	6.5	6.6	7.0	2.29
Drumnagair	7.6	7.4	6.3	5.5	6.5	6.5	2.54

The similarity between Inschfield and Ladywell can be seen from the heat of wetting figures both before and after treatment with hydrogen peroxide. The resemblance between Logienewton and Drumnagair, two soils that are dissimilar in other respects, points to the need of a further investigation into the heat of wetting of the clay fraction before this could be used as a means of characterizing soils. The heat of wetting of the hydrogen peroxide treated soils is considerably less than that of the untreated soils, pointing to the important part played by organic colloids in heat of wetting. If the organic material is not removed the hydrogen clay gives a lower value than the calcium clay, but if the organic material is first removed there is practically no difference between the values of the hydrogen and calcium clays prepared from the residues. This may mean that if the nature of the adsorbed ion has an effect on the heat of wetting it is chiefly on the organic fraction.

The $\text{SiO}_2/\text{R}_2\text{O}_3$ ratios show the resemblance of Ladywell to Inschfield and of Danestone to Craigiebuckler. There is a tendency for the base-exchange capacity of the soils to increase as the $\text{SiO}_2/\text{R}_2\text{O}_3$ ratio of the clays decreases. [This may have a bearing on the utilization of the lime

and on the liming factor. A low base-exchange capacity coupled with a high initial percentage saturation may result in a low fixation of added lime and consequently a high liming factor: at Drumnagair only 50% of the heavy application is utilized and the factor is 3. A high exchange capacity and low initial saturation may result in a greater fixation of the lime and a low factor: at Inchfield 80% of the lime is utilized and the factor is 1.5.]

Field and laboratory tests point to an increase in the permeability of the soil due to the flocculation of the clay particles following the application of lime. The results, which are reported elsewhere (Whelan, 1937), show that the increase varies directly with the amount of lime applied and that the effect is still apparent three years after liming.

It is of interest to make a general comparison of the seven soils. The most important characteristics from a practical point of view being the liming factor and the retention of the added lime, the soils then fall into three groups: Inchfield, Ladywell and Logienewton give nearly theoretical response in the field, the two granitic soils—Danestone and Craigiebuckler—show a higher liming factor, but this shows no increase between the first and the third year after liming; Drumnagair and Overhill also have a high factor and this increases relatively rapidly after application owing to the leaching of the calcium. Generally the fundamental soil properties, e.g. the clay content, place the soils in the same order, although with other properties as criteria, e.g. the $\text{SiO}_2/\text{R}_2\text{O}_3$ ratio of the clay, the order of the last two groups of soils may be reversed. The secondary properties such as base-exchange capacity, heat of wetting and hygroscopicity also show a tendency to place the soils in the same order. The results indicate that as regards that important practical problem, the liming factor, useful information might be gained from a study of the physical and chemical properties of the colloidal material from different soil types.

SUMMARY

An investigation into the effects of lime on five acid soils in north-east Scotland has been continued during the second and third years after the application of lime and also extended to two other centres.

On four of the original soils the full effect of the lime on the surface soil has been largely maintained up to the end of the third year. The fifth, a soil of low base-exchange capacity, shows a considerable loss of lime by the end of the second year.

The lime leached from the top nine inches of soil appears to be re-

tained to only a slight extent in the second nine inches. This was particularly noticeable on a soil of low base-exchange capacity, where, during the two years after liming, the percentage saturation of the subsurface soil showed an increase from 64 to 67 %, and the surface soil a decrease from 92 to 74 %.

The existence of a low liming factor (1.5), previously found to hold for a geologically basic soil, has been verified and found to apply also to a soil derived from slate.

A fundamental property of the soils with a low liming factor is the high content of inorganic and organic fine material. Secondary characteristics that distinguish these soils from the others are the relatively high values for hygroscopicity and heat of wetting.

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PHOTOSYNTHESIS IN THE EAR OF BARLEY, AND THE MOVEMENT OF NITROGEN INTO THE EAR

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(With One Text-figure)

INTRODUCTION

THE physiology of the growth of the grain of cereals, and of the processes which determine the composition of the mature grain, is not fully understood. For barley the problem is of great practical importance, because the malting quality of the grain and its market value vary widely with its composition, and particularly with its nitrogen content. Though much work has been done to elucidate the relationship between environmental factors during the growth of the barley plant and the nitrogen content of the grain at harvest (Russell & Bishop, 1933), little is known of the internal factors which control the relative rates of movement of carbohydrate and nitrogen compounds into the grain.

In normal field conditions the nitrogen content of the grain of cereals expressed as percentage of dry matter varies only slightly as the grain grows, the tendency being for a fall in nitrogen percentage in the early stages, followed by a rise approximately to the initial level at maturity. In the experiment of Brenchley (1912) on barley, the change was from 1.7 to 1.3 % and back to 1.7 %, and in that of Bishop (1930) from 1.54 to 1.36 % and back to 1.52 %. Approximate calculations of the nitrogen content of the material entering the grain in successive intervals of time were made by Brenchley, who found that this was relatively constant until the closing stages, when it rose appreciably. This rise, and the tendency of the nitrogen content of the grain itself to rise, were ascribed by Brenchley & Hall (1909) to "continued loss of non-nitrogenous matter by respiration". The variations found by these authors for wheat were greater than for barley, the nitrogen content falling in one experiment from 2.48 to 1.6 % and then rising to 1.75 %. Woodman & Engledow (1924), working on wheat, found a similar drift of nitrogen content, but in the mature grain it reached a slightly higher level than the initial

values. Knowles & Watkin (1931) determined the change with time in the nitrogen content of the entire ear of wheat. Their results differ from those of the other authors cited, for they recorded a steady fall which was not followed by a rise in the later stages.

Bishop (1930) concluded from his results that "the nitrogen percentage remains approximately constant, which shows that nitrogen compounds and carbohydrates enter the grain in approximately constant relative proportions", apparently regarding the observed drift as insignificant. Brenchley's data and her explanation for the upward drift with maturity may be taken as supporting this view.

It might be assumed that all the material which passes into the grain is derived from the mobilization of reserves accumulated in the shoot before the time of flowering. The constancy of composition of this material throughout the development of the grain might then be taken as indicating a mass transference from shoot to ear of a mixture of nitrogen compounds and other substances, in the proportions in which they were present in the available reserves. It is known that almost all the nitrogen which enters the grain must be mobilized from other tissues, for several workers have shown that little nitrogen is taken up by the plant after the beginning of ear formation, and at maturity 60-80% of the nitrogen content of the aerial part of the plant is to be found in the grain. The assumption is not true, however, of the carbohydrate supply to the ear, most of which is derived from photosynthesis during the time when the ear is developing. For example, data for barley given by Archbold (1938) show that from the end of June to the end of July when the ear was growing rapidly, the dry weight of the stem was steadily increasing, and the dry weight of the leaves was nearly constant. As the increase in dry weight of the ear was not accompanied by a depletion of dry matter in the stem and leaves, little if any of the carbohydrate which entered the ear can have been derived from reserves existing in the stem and leaves before the beginning of rapid growth of the ear.

It is clear, therefore, that the approximate constancy of the nitrogen percentage of the grain during its development is not the result of a movement of nitrogen compounds and carbohydrate to the grain at rates proportionate to the amounts of these compounds present as reserves in the stem and leaves before the time of flowering. An alternative hypothesis is that the movement of nitrogen compounds into the grain is dependent on a simultaneous migration of carbohydrate, or vice versa. If this is true, a drastic restriction of the carbohydrate supply to the ear should be accompanied by a corresponding reduction of total nitrogen

content. On the other hand, as the amount of nitrogen in the plant, and therefore presumably the amount available for movement to the ear, is fixed at the beginning of ear formation, and the amount of carbohydrate available must be dependent on climatic conditions while the ear is growing, it is possible that the approximate constancy of composition of the developing ear may be merely a consequence of the particular conditions of soil and climate during the normal growth of the plant. If this is so, a restriction of the supply of carbohydrate to the ear should cause little, if any, change in the amount of nitrogen which enters the ear.

If the leaves and stem were the only sources of carbohydrate supply, the paths of movement of carbohydrate and nitrogen compounds to the ear might be identical, and an interdependence of the rates of movement of carbohydrate and nitrogen compounds would not be inconceivable. It is probable, however, that photosynthesis in the ear itself may supply some part of the carbohydrate which passes into the grain. If this part is a considerable fraction of the whole carbohydrate supply, an interdependence of the rates of entry of carbohydrate and nitrogen compounds into the grain could only be imposed by conditions in the grain itself, for the sources and paths of movement of carbohydrate and nitrogen compounds would be different.

By comparing the yield of grain produced by wheat plants in which the ear was shaded, with the yield of unshaded controls, Boonstra (1929) found that 27% of the total grain dry weight was derived from photosynthesis in the ear. Smith (1933) has made similar experiments on wheat, and his estimate of the contribution of assimilation in the ear is somewhat higher, amounting to 41% of the total dry weight of grain. He points out, however, that this is a maximum estimate, because it represents the dry weight of grain produced by the ear alone when the plant is defoliated and the shoot darkened, and in these conditions "the grain may be expected to extract the maximum possible amount of carbohydrate from the glumes, etc., when other sources of supply—leaves and stems—are put out of action".

The results of these workers justify the conclusion that in wheat about 30% of the dry matter in the mature grain is produced by assimilation in the ear.

No similar measurements appear to have been made on barley. The ear of barley forms a greater proportion of the whole plant than in wheat, and in the two-row varieties the surface of the ear freely exposed to light and the external atmosphere is probably greater relative to the size

of the ear than in wheat. The long awns of the common varieties of barley may also make some contribution to assimilation in the ear (Harlan & Anthony, 1920). For these reasons it is possible that in barley an even greater proportion of the total assimilation is attributable to the ear than in wheat.

The present work was designed to obtain information on these two questions, namely, what proportion of the carbohydrate supply to the ear is provided by photosynthesis in the ear itself, and whether nitrogen compounds and carbohydrate pass into the ear independently or at rates dependent on each other. Barley plants were grown in pot culture and, as soon as possible after ear emergence, the ear or shoot or the whole plant was darkened by means of an opaque shade, unshaded controls being retained. By this means it is possible to assess the contributions made by assimilation in the ear and in the shoot to the total increase of dry weight of the plant after ear emergence, and to test whether or not they are independent of each other. The measure of assimilation is a net one, representing the balance of true assimilation and respiration. There are two obvious sources of error in the shading method. Shading will affect the temperature conditions of the plants and thus their respiration, and may also cause differences in the rate of senescence, so that the length of time during which the plant is capable of assimilating may vary with the different shading treatments. These possibilities will be discussed later. The change in dry weight of the completely shaded plants gives an indication of respiration loss during the experimental period.

Shading the different parts of the plant varies the amount of carbohydrate available for the growth of the ear, so that the data provide information on the relation between movement of nitrogen into the ear and increase in carbohydrate content. The nitrogen supply was also varied by the addition of nitrogenous fertilizers to some pots, and in the 1937 experiment, by varying the time of application of the nitrogenous fertilizer, in order that the results might be applicable to a wide range of conditions of nitrogen nutrition. It has been found in wheat (Watson, 1936) that the uptake of nitrogen by the plant is almost as great when the nitrogen is supplied very late, just before ear emergence, as when supplied earlier, but with late applications a greater proportion of the nitrogen taken up passes into the ear.

EXPERIMENTAL PROCEDURE

METHOD OF SHADING

The shades used (Fig. 1) were tubes of about $1\frac{1}{2}$ in. diameter, made of two layers of cartridge paper, the outer white and the inner black. This arrangement was adopted to avoid the excessively high temperatures inside the tubes when in bright sunlight, which would have been developed if black tubes had been used. As a further precaution the two layers were separated by an air gap of about $\frac{1}{8}$ in. by introducing washers of cardboard held by paper clips between them. Ventilation was assisted by punching a series of holes along the length of the tube so arranged that the holes in the two layers did not coincide. In the 1936 experiment a separate shade was used for each plant, but in the 1937 experiment one shade was used for a group of three plants.

EXPERIMENT 1, 1936

Sixteen glazed earthenware pots, 8 in. in diameter, were set up on 23 March 1936, each containing 25 lb. of Rothamsted soil to which was added 2.5 g. of di-potassium phosphate. Twelve seeds of a pure line of Spratt-Archer barley, selected to weigh between 0.04 and 0.05 g., were sown per pot. In early May the yellowish colour of the plants and the small number of tillers produced indicated that the supply of nitrogen was deficient, and accordingly a basal application of 1 g. of sodium nitrate was given to every pot.

The experimental treatments were as follows:

No N = no additional nitrogenous fertilizer,

N = 5 g. sodium nitrate per pot (68.6 mg. N per plant) applied in two equal doses on 12 June and 19 June.

There were eight replicate pots for each nitrogen treatment.

O = unshaded,

S = shoot (leaves and stem) shaded,

E = ear shaded,

SE = both ear and shoot (whole plant) shaded.

These treatments were applied to two plants selected at random in each pot.

The shades were applied on 3 July. At this time all ears were partially emerged from the sheath of the highest leaf, but few were fully emerged.



Fig. 1. Method of shading. Exp. 2, 1937. From left to right the treatments are: unshaded, shoot shaded, ear shaded, whole plant shaded.

Where ear or stem alone was shaded, the ear was pulled out from the side of the leaf sheath, if it had not already emerged fully. Most of the plants produced only one ear; about one-quarter of the plants had a second, usually much smaller, ear. The effects of the shading treatments on the main shoot only will be considered in detail.

A sample of one plant per pot was taken on 3 July to provide an estimate of dry weight and nitrogen content at the beginning of the experiment. The treated plants were harvested on 11–12 August. The plants were cut off at soil level, and the ears were cut off at the basal notch. Main shoots and side shoots were kept separate. The main shoots of the two plants which received the same treatment in each pot were combined to make a single sample, and the side shoots were bulked to give one sample for each treatment in the experiment.

Ear and shoot samples were weighed fresh, and again after drying in a steam oven at 100° C. Nitrogen content was determined on the dried samples, after bulking to give duplicate samples for each treatment so as to reduce the analytical work to a minimum. The produce of corresponding treatments from the same four pots was combined to make the bulked samples, so that the comparison of nitrogen content for the shading treatments was kept free of pot differences. The weight of roots was not recorded.

It was not found possible to separate the grain from the ear, because of the large number of samples on which this would have had to be done. For the present purpose it is sufficient to consider the ear as a whole.

Results

The means for individual treatments, for the main shoot only, are given in Tables I–V. The data were examined statistically by the analysis of variance method. Each analysis gave two estimates of error, (1) obtained from the residual variance between pots, and (2) from the residual variance within pots. The standard errors derived from these variances are given in each table. Standard error (1) derived from the between

Table I. *Exp. 1. Samples taken at beginning of the experiment. Main shoot*

	Dry weight per plant g.			Nitrogen content per plant mg.			Nitrogen as % of dry matter	
	Ear	Shoot	Total	Ear	Shoot	Total	Ear	Shoot
No N	0.43	0.71	1.14	5.68	5.66	11.34	1.32	0.80
N	0.42	0.92	1.34	8.90	23.47	32.37	2.12	2.55
Mean	0.42	0.81	1.24	7.29	14.56	21.85	—	—

pots variance is appropriate for comparisons of the nitrogen treatments, and standard error (2) derived from the within pots variance is appropriate for comparisons of the shading treatments and their interactions with the nitrogen treatments.

(1) *Dry weight per plant* (Table II).

(a) *Ear*. The dry weight of the ear was significantly greater in the plants receiving nitrogen than in those without. It was reduced to the same extent by shading either ear or shoot, and the reduction was greater in the nitrogen-treated plants. For the plants without added nitrate, the reduction was 24% of the dry weight of the unshaded ears, and for the nitrate-treated plants it was 34%. The effect of shading both ear and shoot was slightly less than the sum of the effects of shading ear and shoot separately, but not significantly so; that is, the reduction produced by shading the ear was approximately the same, whether the shoot was also shaded or not. The dry weight of the ear increased during the period of shading with all treatments (cf. Tables I and II), but the increase was very small in the completely shaded plants (treatment SE).

Table II. *Exp. 1. Dry weight (g.) per plant. Main shoot*

	Ear					Shoot					Total				
	O	S	E	SE	Mean	O	S	E	SE	Mean	O	S	E	SE	Mean
No N	0.79	0.59	0.61	0.44	0.61	0.68	0.75	0.69	0.68	0.70	1.46	1.34	1.30	1.12	1.30
N	1.08	0.74	0.74	0.47	0.76	0.84	0.70	0.74	0.74	0.76	1.92	1.45	1.48	1.21	1.52
Mean	0.93	0.67	0.67	0.46	0.68	0.76	0.73	0.72	0.71	0.73	1.69	1.39	1.39	1.16	1.41
s.e. individual	(1) ± 0.046					(1) ± 0.039					(1) ± 0.110				
treatment means	(2) ± 0.033					(2) ± 0.029					(2) ± 0.031				

(b) *Shoot*. The dry weight of the shoot was significantly greater in the plants receiving nitrogen than in the others. On the mean of the nitrogen treatments, no significant change in the dry weight of the shoot was produced by shading either ear or shoot. When the nitrogen treatments are considered separately the results are less regular. In the plants the ear of which was unshaded, shading the shoot increased the dry weight of the shoot of the plants without nitrogen, but decreased it when nitrogen was applied. This appears in the analysis of variance as a significant second order interaction, and no satisfactory explanation of this result can be offered. The dry weight of the shoot at harvest was less than at the beginning of the shading treatments (cf. Tables I and II), indicating that the growth of the ear was at least partly at the expense of material already present in the shoot.

(c) *Total of ear and shoot.* The differences between treatments in total dry weight are mainly traceable to differences in the ear. The total dry weight was reduced equally by shading ear or shoot, and the reduction was greater in the plants which received the nitrogen treatment. The second order interaction of the shading and nitrogen treatments was significant, and this is the same effect as was found for the shoot.

(2) *Dry matter as percentage of fresh weight* (Table III).

(a) *Ear.* The dry matter as percentage of fresh weight of the ear was increased by shading the ear in the plants which did not receive the nitrate application, but not in the nitrogen-treated plants. Shading the shoot had no effect.

Table III. *Exp. 1. Dry matter as percentage of fresh weight. Main shoot*

	Ear					Shoot				
	O	S	E	SE	Mean	O	S	E	SE	Mean
No N	85.9	87.6	91.3	92.0	89.2	73.3	81.4	71.0	82.2	77.0
N	88.1	88.3	88.5	87.1	88.1	48.5	87.1	46.7	89.1	67.9
Mean	87.0	88.0	89.9	89.7	88.6	60.9	84.3	58.9	85.7	72.4
S.E. individual treatment means	(1) ± 0.92 (2) ± 1.38					(1) ± 5.89 (2) ± 2.42				

(b) *Shoot.* The dry matter as percentage of fresh weight of the shoot was increased by shading the shoot, but not by shading the ear. The effect of shading the shoot was greater in the nitrogen series of plants, because the dry matter percentage of the shoots which were not shaded was much lower, and that of the shaded shoots slightly higher than in the plants without nitrate. The outstanding effect here is the low dry matter content of the unshaded shoots of the nitrogen-treated plants. Many of these retained their green colour at harvest, and it was obvious by inspection that they had dried out to a much less extent than those of other treatments.

Interpreting these differences as showing variations in the rate of ripening and drying of the plants, it appears that, broadly, the nitrogen application delayed ripening, and shading hastened the ripening of the part of the plant shaded, but not of the rest of the plant.

(3) *Total nitrogen content, mg. per plant* (Table IV).

(a) *Ear.* The nitrate application approximately doubled the nitrogen content of the ear, for all shading treatments. Shading the ear reduced its nitrogen content slightly, but shading the shoot had no effect on the

nitrogen content of the ear. The effect of shading the ear was greater in the plants which received the nitrate treatment than in the untreated plants. The reduction in nitrogen content amounted to 8% of the nitrogen content of the unshaded ear, in the plants which received no added nitrate, and to 17% in the nitrate-treated plants. It should be noted that this was much smaller than the percentage reduction of dry weight caused by shading the ear.

Table IV. *Exp. 1. Nitrogen content per plant (mg.). Main shoot*

	Ear					Shoot					Total				
	O	S	E	SE	Mean	O	S	E	SE	Mean	O	S	E	SE	Mean
No N	10.5	10.2	9.3	10.1	10.0	2.4	2.6	2.7	2.6	2.6	12.9	12.9	12.0	12.7	12.6
N	23.0	24.4	20.2	19.2	21.7	14.1	10.5	11.0	13.1	12.2	37.1	34.9	31.1	32.3	33.9
Mean	16.8	17.3	14.7	14.6	15.9	8.2	6.6	6.8	7.9	7.4	25.0	23.9	21.5	22.5	23.2
s.e. individual treatment means	(1) ± 0.48 (2) ± 0.82					(1) ± 0.80 (2) ± 0.33					(1) ± 1.17 (2) ± 0.80				

About half the nitrogen content of the ear at harvest was already present in the ear at the time when the shading treatments were begun (Table I).

(b) *Shoot.* The nitrogen content of the shoot of the plants which did not receive the nitrate application was very low, and the nitrate application caused a fivefold increase. The nitrogen content of the shoot at harvest was only about half that present at the time when shading was begun.

The effects of shading on the nitrogen content of the shoot showed the same variation with the nitrate treatments as was found for dry weight. In the absence of added nitrate the effects were small, and shading either ear or shoot gave a slightly higher nitrogen content than shading both or neither. In the plants receiving the nitrate treatment, the reverse effect was found, and its magnitude was greater.

(c) *Total of ear and shoot.* The nitrogen content of the whole main shoot was but little greater at harvest than at the time when shading was begun, so that the uptake of nitrogen during the course of the experiment was very small. The increase in nitrogen content of the ear was, therefore, almost entirely at the expense of the shoot. The unshaded plants which received nitrate should perhaps be excepted from this statement, for in these there was fairly clear evidence of an appreciable nitrogen uptake during the experiment.

As the effects of shading on the nitrogen content of the shoot were small, the differences due to shading found in the nitrogen content of

the whole main shoot (total of ear and shoot), reflect mainly the effects found in the ear.

In the plants which received the nitrate application, the mean recovery of added nitrogen in the whole plant including the side shoots was 49%.

(4) *Nitrogen content as percentage of dry matter* (Table V).

(a) *Ear*. Shading both ear and shoot increased the nitrogen content as percentage of dry matter. The effect of shading the shoot was the greater, for though both shading treatments reduced the dry weight of the ear to the same extent, shading the shoot did not affect the total amount of nitrogen in the ear, while shading the ear slightly reduced it.

Table V. *Exp. 1. Nitrogen as percentage of dry matter. Main shoot*

	Ear					Shoot				
	O	S	E	SE	Mean	O	S	E	SE	Mean
No N	1.34	1.73	1.53	2.29	1.72	0.35	0.36	0.39	0.38	0.37
N	2.13	3.28	2.73	4.08	3.06	1.67	1.49	1.48	1.78	1.60
Mean	1.73	2.51	2.13	3.19	2.39	1.01	0.92	0.93	1.08	0.99
S.E. individual treatment means	(1) ± 0.042 (2) ± 0.052					(1) ± 0.012 (2) ± 0.031				

Nitrogen as percentage of dry matter was much higher in the nitrogen-treated plants, as the increase in dry weight caused by the nitrogen treatment was proportionately much less than the increase in nitrogen uptake.

(b) *Shoot*. In the plants which received no additional nitrate, the nitrogen content as percentage of dry matter was very low, and varied only slightly between the shading treatments. In the nitrate-treated plants the differences were greater, and here shading either ear or shoot separately caused a decrease, while shading both ear and shoot caused a slight increase. This is a result of the same nature, and presumably attributable to the same cause, as those found for the dry weight and the total amount of nitrogen in the shoot.

(5) *Side shoots* (Table VI).

The side shoots of each replicate were not weighed and analysed separately, so that it is not possible to test the significance of differences between treatments. The results are summarized in Table VI. The dry weight of side shoot per plant at harvest was very small in the plants which did not receive the nitrate application. It was greater in the nitrate-treated plants, amounting to about one-third of the dry weight of the main shoot.

Table VI. *Exp. 1. Side shoots*

At beginning of exp.	No. per plant	Dry weight per plant g.			Nitrogen content per plant mg.			Nitrogen as % of dry matter	
		Ear	Shoot	Total	Ear	Shoot	Total	Ear	Shoot
No N	0.5	0.08	0.19	0.27	1.3	1.7	3.0	1.58	0.91
N	0.3	0	0.20	0.20	0	5.4	5.4	—	2.71
Mean	0.4	0.04	0.19	0.23	0.6	3.6	4.2	—	—
At harvest									
No N	0.2	0.03	0.05	0.08	0.5	0.2	0.7	1.95	0.47
N	0.5	0.17	0.36	0.53	5.6	7.3	12.9	3.55	2.02
Mean	0.3	0.10	0.20	0.30	3.0	3.8	6.8	—	—

The side shoot was usually shorter than the main shoot, and consequently with treatment S the whole side shoot was shaded, and with treatment E it was unshaded. Treatments S and SE caused a decrease in the dry weight and nitrogen content of the ear of the side shoot, but had little effect on shoot dry weight. All the shading treatments tended to increase the nitrogen content of the shoot.

Nitrogen as percentage of dry matter was always slightly higher in the side shoot than in the corresponding part of the main shoot.

EXPERIMENT 2, 1937

Forty-four glazed earthenware pots, 8 in. in diameter, were set up on 8 April 1937, each containing 24 lb. of Woburn soil to which 2.5 g. of di-potassium phosphate was added. They were sown with seed of a pure line of Spratt-Archer barley selected to weigh between 0.04 and 0.05 g., retaining twelve plants per pot after germination.

The plants tillered much more freely than in the 1936 experiment, and this, together with their dark green colour, suggested that the available supply of nitrogen in the soil was much greater than in the 1936 experiment. The Woburn soil used had lain in a bin for nearly a year. It was the only soil available at the time when the pot cultures were set up, for owing to continued wet weather it was impossible to obtain a supply of Rothamsted soil from the field. To avoid complications due to the high shoot number, all shoots other than the main shoot of each plant were removed on 15 July. The plants which received a late nitrogen dressing produced a few small tillers later and these were removed as they appeared.

The nitrogen treatments used were:

N_0 = no nitrogenous fertilizer.

N_E = 5 g. sodium nitrate per pot (68.6 mg. N per plant), applied early, in two equal doses, on 10 and 15 May.

N_L = 5 g. sodium nitrate per pot, applied late, in two equal doses, on 28 June and 3 July.

Fourteen pots were used for treatment N_0 , and fifteen each for treatments N_E and N_L .

The shading treatments were the same as in the 1936 experiment. The shades were applied as soon as possible after the beginning of ear emergence on 15–16 July, to ten pots of each of the three nitrogen treatments. Each shade enclosed three plants, the group of three neighbouring plants being selected at random.

The remaining pots (four of treatment N_0 , and five of each of treatments N_E and N_L) were harvested on 16 July (sampling 1) to give an estimate of dry weight and nitrogen content at the beginning of the experiment.

Five pots of each nitrogen treatment were harvested on 28 July (sampling 2), and the remainder on 13 August (sampling 3). Fresh and dry weights of ear and shoot were recorded for each treatment (three plants) in each pot. As in Exp. 1, the dried plants were bulked to give duplicates for each treatment at each harvest for the determination of nitrogen content. Of the two samples, one consisted of the produce of three pots and the other of two pots.

Results

The results are given in Tables VII–X as means for each treatment combination. A separate statistical analysis was made of the data in each table for sampling 1, taken at the beginning of the experiment. Samplings 2 and 3 were combined in a single analysis, except for the data on dry matter as percentage of fresh weight, which were analysed separately for each sampling, because the values for samplings 2 and 3, and consequently the magnitudes of the standard errors, differed widely.

As in Exp. 1, two standard errors are given in each table: (1) derived from the residual variance between pots is appropriate for comparisons involving sampling times and nitrogen treatments, and (2) derived from the residual variance within pots is appropriate for testing differences between shading treatments and their interactions.

(1) *Dry weight per plant* (Table VII).

(a) *Ear*. In all three samplings, the dry weight of the ear was less where nitrogen was given early than when it was given late or withheld. The late nitrogen application had no appreciable effect on ear dry weight. Between samplings 1 and 2 the dry weight of the ear was doubled, and there was a further small but significant increase between samplings 2 and 3.

Table VII. *Exp. 2. Dry weight per plant (g.)*

		Ear					Shoot					Total				
Sampling 1		N _O	0.56	1.04	1.60		N _E	0.40	1.06	1.46		N _L	0.51	1.02	1.53	
		Mean	0.49	1.04	1.53											
		S.E.	±0.034	±0.039	±0.065											
		Ear					Shoot					Total				
		O	S	E	SE	Mean	O	S	E	SE	Mean	O	S	E	SE	Mean
Sampling 2	N _O	1.12	1.06	1.06	0.71	0.99	0.99	0.91	0.94	0.81	0.91	2.11	1.97	2.00	1.52	1.90
	N _E	0.89	0.70	0.67	0.54	0.70	0.93	0.85	0.87	0.79	0.86	1.82	1.55	1.54	1.33	1.56
	N _L	0.98	0.88	0.80	0.83	0.87	1.01	0.82	0.85	0.89	0.89	1.99	1.70	1.65	1.72	1.76
	Mean	1.00	0.88	0.81	0.69	0.85	0.98	0.86	0.89	0.83	0.89	1.97	1.74	1.73	1.52	1.74
Sampling 3	N _O	1.10	1.08	0.94	0.81	0.98	0.80	0.81	0.85	0.74	0.80	1.90	1.89	1.79	1.55	1.78
	N _E	0.98	0.86	0.83	0.68	0.84	0.86	0.84	0.89	0.81	0.85	1.84	1.70	1.72	1.48	1.69
	N _L	1.19	1.02	1.05	0.75	1.01	0.98	0.84	0.95	0.81	0.89	2.17	1.86	2.00	1.56	1.90
	Mean	1.09	0.99	0.94	0.75	0.94	0.88	0.83	0.89	0.78	0.85	1.97	1.82	1.84	1.53	1.79
s.e. individual treatment means		(1)	±0.091	(2)	±0.071	(1)		±0.063	(2)	±0.044	(1)		±0.144	(2)	±0.118	

Shading either ear or shoot reduced the dry weight of the ear at samplings 2 and 3, and the effect of shading the ear was slightly greater than that of shading the shoot, but not significantly so. The reduction in the dry weight of the ear when both ear and shoot were shaded was slightly but not significantly greater than the sum of the effects of shading ear and shoot separately, so that the effects of the two shading treatments were independent.

The effects of shading did not vary significantly with sampling time or nitrogen treatment. The shading treatments had produced their full effects at sampling 2, for the increase in dry weight of the ear between samplings 2 and 3 was too small to show significant variation with shading treatments.

(b) *Shoot*. The dry weight of the shoot was not significantly affected by the nitrate application. It decreased considerably between samplings 1 and 2, but the subsequent small decrease between samplings 2 and 3, which was only apparent where no nitrate was applied, was not significant.

Shading the ear and shading the shoot both reduced the dry weight

of the shoot, and their effects were independent of each other. The reduction was twice as great where the shoot was shaded, as where the ear was shaded. There was no clear evidence that the effects of shading varied with nitrogen treatment or sampling time.

(c) *Total of ear and shoot.* The early application of nitrogen caused a marked reduction of total dry weight, while the late application had no appreciable effect. There was a large increase in dry weight between samplings 1 and 2, but little subsequent change. The interaction between sampling times and nitrogen treatment was not significant, but the results suggest that over the whole period of the experiment the dry weight of the plants which received the late nitrogen application increased more than that of the others.

Shading the ear and shading the shoot reduced the total dry weight almost equally, and the reduction caused by either treatment was independent of the other, and of nitrogen treatments and sampling times.

(2) *Dry matter as percentage of fresh weight (Table VIII).*

(a) *Ear.* At the beginning of the experiment, in sampling 1, the early nitrogen application had caused a small reduction in dry matter as percentage of fresh weight, that is, an increase of water content, while the later application had no effect. This difference is possibly related to the higher nitrogen content as percentage of dry matter caused by the early nitrogen application.

Table VIII. *Exp. 2. Dry matter as percentage of fresh weight*

Sampling 1		Ear					Shoot				
		N _O	N _E	N _L	Mean	s.e.	N _O	N _E	N _L	Mean	s.e.
		32.8	28.8	32.2	31.3	±0.57	31.9	28.4	30.8	30.4	±0.51
Sampling 2		Ear					Shoot				
		O	S	E	SE	Mean	O	S	E	SE	Mean
	N _O	48.2	45.6	45.2	40.4	44.9	30.9	28.8	29.5	26.6	29.0
	N _E	42.5	46.4	42.0	45.5	44.1	25.1	34.3	26.3	34.2	30.0
	N _L	46.7	44.0	42.0	42.9	43.9	30.5	29.1	28.5	28.9	29.2
	Mean	45.8	45.3	43.1	42.9	44.3	28.8	30.7	28.1	29.9	29.4
Sampling 3		Ear					Shoot				
		O	S	E	SE	Mean	O	S	E	SE	Mean
	N _O	91.1	93.0	89.8	93.6	91.9	46.1	63.1	52.5	68.0	57.4
	N _E	89.7	92.3	91.4	91.9	91.3	34.0	82.0	36.0	84.7	59.2
	N _L	89.7	91.6	90.6	93.4	91.3	33.3	75.2	34.3	82.0	56.2
	Mean	90.1	92.3	90.6	92.9	91.5	37.8	73.4	40.9	78.2	57.6
s.e. individual		Sampling 2 (1) ±2.23 (2) ±1.26					(1) ±2.57 (2) ±1.40				
treatment means		Sampling 3 (1) ±0.69 (2) ±0.71					(1) ±5.67 (2) ±3.97				

At sampling time 2, dry matter as percentage of fresh weight was somewhat higher than at sampling time 1, and the difference between nitrogen treatments had disappeared. Shading the ear caused a decrease whatever the nitrogen treatment. This result is the reverse of that found in Exp. 1. The effect of shading the shoot varied with nitrogen treatment. In the plants receiving the early nitrogen application, shading the shoot increased the dry matter percentage, while in the plants having no added nitrogen or the late application, it caused a decrease.

The differences between treatments were small at sampling time 3, and the dry matter percentages were high. The effects of the shading treatments were almost completely reversed. Shading the ear had no significant effect, the figures actually showing a slight increase. Shading the shoot increased the dry matter percentage, whatever the nitrogen treatment, but the increase was smaller in the plants receiving the early nitrogen application than in the others.

(b) *Shoot*. Dry matter as percentage of fresh weight of the shoot was depressed by the early nitrogen application, at sampling time 1, but the late application had no obvious effect.

At sampling 2, dry matter percentage was close to that found at sampling 1, but it was much higher at sampling 3. Shading the ear produced no significant differences. The effect of shading the shoot varied with the nitrogen treatment. At sampling 2, it caused a depression in the plants without added nitrogen or with a late application, and an increase where the early application was given. At sampling 3, it consistently caused an increase, but the effect was greater where nitrogen was applied, and particularly so where the application was given early.

It is difficult to account completely for the complex effects of the treatments on dry matter as percentage of fresh weight on the basis of the information provided by the experiment itself. Shading is likely to have affected the water relations of the plants in several ways, some of which are mutually antagonistic, so that the differences observed depend on the relative intensity of opposing effects. A consideration of these effects is reserved for the subsequent discussion.

(3) *Nitrogen content mg. per plant* (Table IX).

(a) *Ear*. The nitrogen content of the ear at sampling 1 was not significantly altered by nitrogen treatment; it was slightly lower where nitrogen was given, especially at the early application. In samplings 2 and 3 both nitrogen applications increased the nitrogen content of the ear to approximately the same extent, and the increase was greater

at sampling 3 than at sampling 2. Thus, over the period of the experiment the movement of nitrogen into the ear was more rapid in the plants which received the nitrogenous fertilizer than in those which did not.

Table IX. *Exp. 2. Nitrogen content per plant (mg.)*

						Ear	Shoot	Total												
Sampling 1						N _O	12.9	11.5	21.4											
						N _E	10.8	18.7	29.5											
						N _L	12.1	13.9	25.9											
						Mean	11.9	14.7	26.6											
						s.e.	±0.40	±1.03	+1.35											
						Ear					Shoot					Total				
		O	S	E	SE	Mean	O	S	E	SE	Mean	O	S	E	SE	Mean				
Sampling 2	N _O	19.1	20.3	19.3	17.7	19.1	6.1	5.2	6.1	5.7	5.7	25.2	25.5	25.3	23.1	21.8				
	N _E	22.6	24.8	19.4	21.0	21.9	14.0	11.7	13.8	10.0	12.4	36.7	36.5	33.2	30.9	34.3				
	N _L	22.2	22.6	19.7	26.0	22.6	12.1	7.3	11.0	7.7	9.5	34.3	29.9	30.7	33.7	32.1				
	Mean	21.3	22.6	19.4	21.6	21.2	10.7	8.1	10.3	7.8	9.2	32.0	30.6	29.7	29.3	30.4				
	S.E.																			
Sampling 3	N _O	20.8	21.0	18.6	19.1	19.9	4.9	4.3	5.8	4.0	4.7	25.6	25.3	24.5	23.1	24.6				
	N _E	26.6	27.4	26.6	25.1	26.4	13.4	9.2	12.2	8.3	10.7	40.0	36.5	38.8	33.4	37.2				
	N _L	28.2	25.7	26.4	24.3	26.2	12.1	8.3	10.3	7.1	9.4	40.3	34.0	36.7	31.4	35.6				
	Mean	25.2	24.7	23.9	22.8	24.2	10.1	7.2	9.1	6.5	8.3	35.3	31.9	33.3	29.3	32.5				
	S.E.																			
s.e. individual treatment means		(1) ± 0.82 (2) ± 2.13					(1) ± 0.90 (2) ± 0.61					(1) ± 1.40 (2) ± 2.17								

Shading had no significant effects. There are indications that at both samplings 2 and 3 shading the ear slightly depressed the nitrogen content, and that shading the shoot caused a small increase at sampling 2 and a decrease at sampling 3.

(b) *Shoot.* The nitrogen content of the shoot decreased very greatly between samplings 1 and 2, indicating a rapid translocation of nitrogen to the ear. The fall continued between samplings 2 and 3, but in this period the change was small.

The nitrogen content of the shoot was always highest in the plants which received the early nitrogen application. There was only a small difference at sampling 1 between the plants which were not given the nitrogenous fertilizers and those which had the late application, but the difference was much greater at samplings 2 and 3, showing that proportionately more nitrogen was removed from the shoots of the untreated plants to the ear, than from those to which the late application of nitrogen was given.

Shading the ear caused a small depression of the nitrogen content of the shoot. Shading the shoot caused a greater reduction than shading the ear, and had a greater effect on the plants receiving the nitrogenous fertilizer, than on the untreated plants.

(c) *Total of ear and shoot.* The nitrogen content of the whole plant

(total of ear and shoot) was always higher where the nitrogenous fertilizer was applied early than where it was applied late, and both treatments caused an increase above that of the untreated plants. The differences were small at sampling 1. There was no appreciable uptake of nitrogen in the N_0 series during the period of the experiment, for the total nitrogen content was almost the same at all sampling times. In the plants to which the nitrogenous fertilizer was given, the total nitrogen content increased throughout, but the increase between sampling times 2 and 3 was smaller than that between samplings 1 and 2. There is an indication that nitrogen uptake was more rapid where the nitrogenous fertilizer was applied late than where it was applied early.

Shading the ear and shading the shoot caused almost equal depressions of the total nitrogen content, and their effects were independent of each other. Inspection of the data suggests that the effect of shading was greater on the plants which received nitrogen, but this difference was not significant.

(4) *Nitrogen content as percentage of dry matter* (Table X).

(a) *Ear*. The nitrogen content as percentage of dry matter of the ear in unshaded plants varied only slightly between samplings. It was somewhat lower at samplings 2 and 3 than at sampling 1. The differences between samplings 2 and 3 were small and not significant. Nitrogen percentage was always highest in the plants which received the early application of nitrogen, and higher where the late application was given than in the unmanured plants.

Table X. *Exp. 2. Nitrogen as percentage of dry matter*

		Ear					Shoot					
Sampling 1		N _O					N _O					
		N _E					N _E					
		N _L					N _L					
		Mean					Mean					
		s.e.	±0.068					±0.083				
		Ear					Shoot					
		O	S	E	SE	Mean	O	S	E	SE	Mean	
Sampling 2	N _O	1.67	1.90	1.82	2.46	1.96	0.61	0.57	0.65	0.69	0.63	
	N _E	2.55	3.43	3.10	3.82	3.23	1.53	1.37	1.59	1.25	1.44	
	N _L	2.37	2.53	2.44	3.12	2.62	1.22	0.88	1.30	0.86	1.07	
	Mean	2.20	2.62	2.45	3.14	2.60	1.12	0.94	1.18	0.93	1.05	
Sampling 3	N _O	1.87	1.95	1.93	2.35	2.03	0.60	0.52	0.67	0.53	0.58	
	N _E	2.55	3.21	3.14	3.75	3.16	1.52	1.09	1.35	1.03	1.25	
	N _L	2.35	2.52	2.50	3.21	2.65	1.21	0.98	1.07	0.88	1.04	
	Mean	2.26	2.56	2.52	3.11	2.61	1.11	0.86	1.03	0.82	0.96	
s.e. individual treatment means		(1) ±0.030 (2) ±0.032					(1) ±0.017 (2) ±0.022					

Shading the ear and shading the shoot both caused an increase in nitrogen percentage, because they markedly decreased the ear dry weight but had little effect on the total amount of nitrogen present. Each shading treatment had a greater effect on nitrogen percentage in the presence of the other. The reason for this is that although the absolute reduction of dry weight caused by shading the ear was the same whether the shoot was shaded or not, the reduction was greater, when expressed as a fraction of ear dry weight, when the shoot was also shaded.

The effect of shading on nitrogen percentage was greater in the plants receiving the early application of nitrogen than in the others. This interaction was significant, but has no obvious explanation. It is attributable entirely to the low value for the unshaded plants which received an early nitrogen application.

(b) *Shoot.* Nitrogen as percentage of dry matter in the shoot declined between samplings 1 and 2, showing that the loss of nitrogen was proportionately greater than the loss of dry matter. The difference between the values for samplings 2 and 3 was very small. Addition of the nitrogenous fertilizer consistently increased the nitrogen percentage, and the early application had a greater effect than the late.

Shading the ear did not affect the nitrogen percentage in the shoot, because it reduced the dry weight and the total amount of nitrogen in the shoot in approximately the same proportion. Shading the shoot caused a small depression of nitrogen percentage, for it caused a proportionately greater reduction in the amount of nitrogen in the shoot than in dry weight. The effect of shading the shoot was greater in the plants which received the nitrogenous fertilizer than in the unmanured plants, where it was very small.

(5) *Side shoots removed at the beginning of the experiment.*

The weights and nitrogen contents of the ear-bearing side shoots removed before the shading treatments were applied are shown in Table XI.

Table XI. *Exp. 2. Side shoots removed at sampling 1. Means per plant*

	Number	Dry weight g.	Dry matter as % of fresh weight	Nitrogen content mg. per plant	Nitrogen as % of dry matter
N _O	1.64	1.37	34.3	19.0	1.39
N _E	2.24	1.58	30.9	31.8	2.02
N _L	1.77	1.49	35.1	25.1	1.68
S.E.	±0.091				

The number of shoots and their dry weight were increased by early application of nitrogen, but the late application had less effect. The increase in dry weight of the side shoots was larger than the decrease found in the main shoot, so that on balance, application of nitrogen gave an increased yield of dry matter in the whole plant, but the differences were very small (Table XII).

Table XII. *Exp. 2. Dry weight per plant at sampling 1.*
Main shoot and side shoots

Treatment	N _O	N _E	N _L
Dry weight per plant g.	2.97	3.03	3.09

There is an indication of a depression of dry matter as percentage of fresh weight by the early nitrogen application, similar to that found in the main shoot at sampling 1. The early application produced a large increase in nitrogen content and nitrogen as percentage of dry matter, and the late application had a similar but smaller effect.

The mean percentage recovery of added nitrogen in the whole plant including the side shoots was 35% for the early application, and 22% for the late application. This was less than in Exp. 1, no doubt because the supply of available nitrogen in the Woburn soil was more abundant than in the Rothamsted soil used in 1936.

DISCUSSION

It is clear that shading has more complex effects on the plant than a mere inhibition of photosynthesis in the part of the plant which is darkened. Some consideration of these secondary effects is necessary, if the results of the experiments are to be interpreted correctly.

The effect of shading on dry matter as percentage of fresh weight is apparently manifested in an acceleration of the ripening and drying out processes associated with senescence in the part of the plant shaded. The effect would be expected to be most marked at the final harvest unless this is delayed so long that normal water loss has proceeded to completion, so that differences in rate of loss are obscured. Thus in Exp. 1, shading the ear decreased the water content of the ear at harvest, and in Exp. 2 at sampling 3, there was evidence of a similar, but smaller and not significant effect. Shading the shoot decreased the water content of the shoot at harvest in both experiments. The explanation of this hastened ripening is not completely clear. It may be attributable partly to a higher temperature inside the shades but this is unlikely to be the

complete explanation. In the shoot it may be due to a more rapid depletion of cell contents by translocation in the absence of photosynthesis leading to earlier senescence and death, but this explanation cannot hold for the ear. Where the effect of shading the shoot in reducing its water content was great, as in Exp. 2 (sampling 3), it is not surprising that a concurrent reduction was produced in the ear, since the ear receives its water supply through the shoot. There is no *a priori* reason why a reduction of the water content of the ear should much affect that of the shoot, and this is in agreement with the results of both experiments.

At sampling 2 in Exp. 2, shading sometimes caused a decrease in dry matter as percentage of fresh weight, i.e. an increase in water content. When the ear was shaded this result was found in the ear whatever the nitrogen treatment, and when the shoot was shaded, it was found in both ear and shoot of the plants which received no nitrogenous fertilizer or the late application. It is possible that this effect was due to a reduction of transpiration loss by shading, which at this early stage in ripening was sufficient to counterbalance the opposing effect of shading in hastening the drying out process of ripening. There is no obvious explanation of the absence of this effect in the plants which received the early nitrogen application.

The application of nitrogen caused an increase of water content in unshaded parts of the plant, and little, or sometimes the reverse, change in shaded parts, so that in general the effects of shading on water content were intensified in the plants with a high nitrogen supply.

The differences in water content produced by shading are not so great as to suggest that the acceleration of ripening, by shortening the period during which the plants were able to assimilate, would seriously affect the estimates of assimilation derived from differences in dry weight between unshaded and shaded plants. The difference in water content of the shoot, between plants with shaded and unshaded shoots, in Exp. 2 (sampling 3) should perhaps be excepted, for it was of a much greater magnitude than any of the other effects. This difference could only invalidate the estimates of assimilation by curtailing the period of respiration loss from the shoot in the shaded plants.

If loss of dry weight by respiration during the period of the experiment were considerable, it should appear as a decline in dry weight of the completely shaded plants. Table XIII shows that the changes in dry weight of these plants were small.

The two experiments were consistent in that the plants without added nitrogen showed a loss, while in those receiving nitrogen there

was a slight gain. If this gain was real, which is very doubtful, it can only be due to translocation from the root exceeding respiration losses. As the mean loss of dry matter was negligible in the completely shaded plants it is unlikely that differential effects of the shading treatments on respiration could introduce any appreciable error into the estimates of net assimilation during the experimental period.

Table XIII. *Loss of dry weight per plant in completely shaded plants*

	Treatment	Initial dry weight g.	Final dry weight g.	Loss g.
Exp. 1 (whole plant)	No N	1.41	1.14	0.27
	N	1.54	1.67	-0.13
				Mean 0.07
Exp. 2	N _O	1.60	1.55	0.05
	N _E	1.46	1.48	-0.02
	N _L	1.53	1.56	-0.03
				Mean 0.0

If translocation of material from the root accounts for any considerable part of the dry weight increase of the ear, it would cause the estimate of net assimilation, derived from the tops of the plants only, to be too high. The drain on material in the roots would be expected to be greater in the shaded plants than in the unshaded, and this would cause an underestimation of the effects of shading on dry weight increase. The experiment gives no information on the amount of translocation from the root. It seems likely to be relatively small, for previous experience with similar pot cultures of Spratt-Archer barley shows that the whole root system forms only about one-fifth of the total plant dry weight.

Table XIV. *Mean reduction of total dry weight per plant caused by shading*

		Ear shaded			Shoot shaded	
		g. per plant	% of ear dry weight of unshaded plants	% of total dry weight of unshaded plants	g. per plant	% of total dry weight of unshaded plants
Exp. 1	No N	0.19 (1)	24	13	0.15 (1)	10
	N	0.34 (1)	31	18	0.37 (1)	18
	Mean	0.26 (2)	28	15	0.26 (2)	15
Exp. 2 (sampling 3)	N _O	0.22 (3)	20	12	0.12 (3)	6
	N _E	0.17 (3)	17	9	0.19 (3)	10
	N _L	0.23 (3)	19	11	0.37 (3)	17
	Mean	0.21 (4)	19	11	0.23 (4)	12

S.E.

(1) ± 0.031 , (2) ± 0.022 , (3) ± 0.118 , (4) ± 0.068

It seems justifiable to conclude that the secondary effects of shading are unlikely to have introduced large errors into the estimates of net assimilation in ear and shoot, derived from the reduction in dry weight caused by shading. The net assimilation by ear and shoot, measured by the effects of shading on the dry weight of the whole plant, are shown in Table XIV.

We may assume that the products of assimilation in the ear remain in the ear, for the decrease in dry weight of the shoot during the experiments indicates that translocation was proceeding from shoot to ear. Assimilation in the ear, measured by the reduction in dry weight of the whole plant when the ear was shaded, accounted for 28% of the final dry weight of the ear in Exp. 1 and 19% in Exp. 2, on the mean of all nitrogen treatments. In previous pot-culture experiments, it has been found that for Spratt-Archer barley the dry weight of the grain is from 80 to 85% of the ear dry weight, over a wide range of ear size. On this basis, assimilation in the ear contributed approximately 35% of the grain weight in Exp. 1 and 25% in Exp. 2. This result is intermediate between those of Boonstra and Smith for wheat (p. 323). It is a minimum estimate, for assimilation must have been proceeding in the ears while they were emerging, before the shades were applied. Shading of the ears throughout their period of emergence was not attempted, because it would have involved damage to the sheath of the flag leaf and to the young ear. The proportion of the total dry weight accounted for by assimilation in the ear did not vary much between the nitrogen treatments.

In both experiments, the effects of shading the ear and shading the shoot on the dry weight of the whole plant were almost identical, showing that after ear emergence ear and shoot make equal contributions to the assimilation of the whole plant. The large proportion of the final dry weight of the plant added after ear emergence, 30% in Exp. 1 and 23% in Exp. 2, illustrates the importance of this late stage of growth in determining the final yield.

Restriction of carbohydrate supply to the grain by shading either ear or shoot caused an increased drain on material in the shoot, reducing its final dry weight, but the effect was small compared with the dry-weight reduction in the ear (Table XV).

The results of both experiments agreed with those of Brenchley (1912) and Bishop (1930) in showing that in normal (i.e. unshaded) plants, the nitrogen content as percentage of dry matter changed only slightly during the growth of the ear. The only exception was that in Exp. 2,

the nitrogen percentage of the ears of plants which received no nitrogenous fertilizer fell considerably between samplings 1 and 2. If, however, the supply of carbohydrate to the ear during the growth of the grain was restricted by shading either ear or shoot, the nitrogen content as percentage of dry matter of the ear was much increased in the final samplings. It is obvious, therefore, that there is no close dependence of the rate of translocation of nitrogen compounds into the ear on the rate of increase in carbohydrate in the ear. The total amount of nitrogen moved into the ear was, in both experiments, only slightly affected by shading. The

Table XV. *Reduction in dry weight (g. per plant) of ear and shoot due to shading. Mean of all nitrogen treatments*

Reduction in dry weight of ...	Ear shaded			Shoot shaded		
	Ear	Shoot	Total	Ear	Shoot	Total
Exp. 1	0.23	0.03	0.26	0.24	0.02	0.26
S.E.	± 0.023	± 0.021	± 0.022	± 0.023	± 0.021	± 0.022
Exp. 2 (sampling 3)	0.19	0.02	0.21	0.15	0.08	0.23
S.E.	± 0.041	± 0.025	± 0.068	± 0.041	± 0.025	± 0.068

small variation of the nitrogen percentage of the ears of normal plants during growth must be regarded, therefore, as fortuitous, and not as an indication that translocation of nitrogen compounds is dependent on increase of carbohydrate in the ear. It is remarkable that the relation should hold over such a wide range of nitrogen content (1.3–2.5% in the present experiments), and there is no obvious explanation why the two apparently independent processes of translocation of nitrogen compounds, and of dry matter increase in the ear should proceed at approximately constant relative rates throughout growth, in a wide range of conditions. As a considerable proportion of the dry matter increase in the ear has been shown to be due to assimilation in the ear, it is clear that the constancy of nitrogen percentage cannot be explained as due to translocation of a mixture of nitrogen compounds and carbohydrate of fixed composition present in the plant at the time of ear formation.

The effects of shading on the total amount of nitrogen present in ear and shoot, though always small relative to the effects on dry weight, differed in the two experiments. In Exp. 1 the largest effect was produced in the ear by shading the ear, while the shoot was not much affected. In Exp. 2, on the other hand, the differences in nitrogen content of the ear were not significant, while in the shoot, shading the shoot caused a reduction. No explanation of this variation of shading effects can be

suggested. It may be related to the difference in level of nitrogen supply, which was higher in Exp. 2 than in Exp. 1.

SUMMARY

Experiments were made in 1936 and 1937 on barley plants grown in pot culture, to determine the effect of shading the ear or the shoot after ear emergence on dry weight and nitrogen content.

It was found that after ear emergence the ear and the shoot (leaves and stem) make approximately equal contributions to the assimilation of the whole plant. In the 1936 experiment 28% of the final dry weight of the ear was accounted for by assimilation in the ear itself, and in the 1937 experiment, 19%. These are minimum estimates, for assimilation must have been proceeding in the ears during emergence, before the shading treatments were applied. The results agree well with similar estimates of the extent of assimilation in the ear made on wheat by other workers.

The effects of shading on the amount of nitrogen present in the plant at harvest were somewhat variable, but they were always small compared with the effects on dry weight. Shading tended to reduce the amount of nitrogen in the ear, but as the dry weight of the ear was reduced to a much greater extent, nitrogen as percentage of dry matter in the ear was increased. It is concluded from this result that translocation of nitrogen compounds to the ear is not closely dependent on the amount of the concurrent increase in dry weight of the ear. It appears that the approximate constancy of nitrogen percentage in the ear and the grain throughout development is a consequence of the particular conditions prevailing during normal growth in the field.

The experiments showed that 20-30% of the dry weight of the whole plant was added after ear emergence, suggesting that climatic conditions during this late stage of growth is of considerable importance in determining the final yield.

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THE COMPOSITION AND DIGESTIBILITY, WHEN FED TO PIGS AND SHEEP, OF POTATO COSSETTES AND POTATO MEAL

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INTRODUCTION

ARTIFICIALLY dried potatoes are being marketed in this country at the present time in two grades, known as potato cossettes and potato meal. "Chat" potatoes are first washed in water tanks provided with revolving paddles and are then elevated into a machine that pulps them into pieces about the size of fingers. The resulting cossettes enter the drier directly from the pulper, forming a layer about 4 in. deep. The wet material passes on an endless conveyer, consisting of a drying belt of perforated sheet metal, through three zones of temperature. The hot-air current has a temperature of 250–260° F. in the first stage and 180–200° F. in the third. The dried cossettes, which are suitable for feeding to sheep and cattle, may be ground to potato meal for use in the rations of pigs.

Table I. *Composition of potato meal and potato cossettes (dry matter basis)*

	Potato meal %	Potato cossettes %	Barley* %	Maize* %
Crude protein	9.76	10.54	11.75	11.38
Ether extract	0.56	0.63	1.76	5.06
N-free extractives	83.38	82.39	78.14	79.54
Crude fibre	2.33	2.36	5.29	2.52
Ash	3.97	4.08	3.06	1.50
Lime (CaO)	0.10	0.09	0.08	0.02
Phosphoric acid (P ₂ O ₅)	0.41	0.44	0.99	0.94
Potash (K ₂ O)	2.43	2.49	0.67	0.46
Soda (Na ₂ O)	0.11	0.14	0.03	0.03
Chlorine	0.34	0.46	0.14	0.08
True protein	5.21	5.60	11.05	10.81
"Amides"	4.55	4.94	0.70	0.57
Moisture content of product as received from factory	10.20	9.80	—	—

* As given in "Rations for Live Stock" (Wood & Woodman, 1936).

It has been the object of the present investigation to secure information about the composition of these potato products and to determine the digestibility of (1) the potato meal when fed to pigs and to sheep, and (2) the potato cossettes when fed to sheep.

COMPOSITION OF POTATO MEAL AND POTATO COSSETTES

The composition, both organic and mineral, of the potato cossettes and meal used in the digestion trials is given, on the basis of dry matter, in Table I. The corresponding figures for barley and maize, two typical cereals that may partially be replaced by the potato products in farm rations, are also shown.

Comments on Table I

No marked differences would be expected between the composition of potato meal and that of potato cossettes, since the former is obtained from the latter by the simple process of grinding. The minor distinctions discernible in the present samples are to be ascribed to the fact that the meal and cossettes had not been produced from the same original consignment of raw potatoes.

Striking similarities will be noted between the composition of the potato products and the cereals, barley and maize. They are all very rich in N-free extractives, in which starch is the chief constituent. They all contain only a moderate percentage of crude protein, but it is to be noted that a much higher proportion of the crude protein in the potato products is present as "amides" than is the case with the cereals; almost one-half of the potato nitrogen is in the form of "amides".

The percentage of ether extract in potato meal and cossettes is very low, amounting to about one-third of that in barley. In the feeding of the bacon pig, the potato products share with barley a distinct advantage over maize, the use of which in more than moderate amount tends to give rise to a soft, oily type of bacon. This undesirable effect is attributed to the presence in maize of a relatively high percentage of unsaturated oil. The oil content of the potato products, on the other hand, is so low that there is little or no danger of the character of the carcass fat being influenced by the oil of the food when these products are used in pig rations. Under such conditions of feeding, body fat is likely to be formed very largely from the starchy constituent, thus ensuring the firm type of fat desired by the curer.

In respect of fibre content, the potato products closely resemble maize and contain less than half the amount present in barley meal.

As with the cereals, the ash content is low. The well-known deficiency of the cereals in lime is shared by the potato products, which contain also only about one-half the amount of phosphoric acid found in barley and maize, but a very much higher percentage of potash. It is particularly to be noted that the potato products are very distinctly richer than the cereals in the important chlorine constituent.

The cold-water extracts of the potato products, filtered absolutely water-clear, gave very distinct reactions for dextrin and contained also small amounts of reducing sugar and soluble starch. The aqueous extracts were also strongly acid to litmus. Indeed, the present consignments of the potato products were distinctly sour to the taste, and determinations of acidity, assuming this to be due to lactic acid, showed the presence of 1.35 g. lactic acid per 100 g. of air-dry meal. Actually, however, only a small proportion of the acid was present as lactic acid, since separate determinations on the aqueous extracts gave only 0.12 g. lactic acid per 100 g. potato meal. Nor could the acidity of the products be accounted for in terms of volatile organic acid, since the steam-distillable acid, per 100 g. meal, required only 5.4 c.c. *N*/10 NaOH for neutralization.

SWELLING POWER OF POTATO MEAL AND POTATO COSSETTES

Since the question of bulk is of importance when designing rations for farm animals, and since both potato meal and potato cossettes are capable of absorbing large amounts of water, it was considered desirable to secure information on the amount of swelling that occurs when the potato products are soaked in water. The results are recorded in Table II, and corresponding figures for barley meal and sugar-beet pulp are given for purposes of comparison.

The technique of the measurements of swelling power was substantially the same as that described by Procter & Wright (1927). In every case, 10 g. of the feeding stuff was weighed into a measuring cylinder

Table II. *Swelling power of potato meal and potato cossettes compared with results for barley meal and sugar-beet pulp*

	"Dry" volume of 10 g. of food	Volume of wet food after		
	c.c.	2 hr. c.c.	4 hr. c.c.	24 hr. c.c.
Barley meal	20	33	34	36
Potato meal	15	40	40	44
Potato cossettes	34	53	53	55
Sugar-beet pulp (unground)	36	90	93	97
Sugar-beet pulp (ground)	18	58	59	63

and, after tapping the cylinder, the "dry" volume was read off. Distilled water at 37° C. was added to bring the volume to 180 c.c., the water and feeding stuff being thoroughly admixed by stirring. The cylinders were then placed in an incubator at 37° C., and the volumes occupied by the wet foods were noted at stated intervals.

From Table II it will be noted that potato meal is very little bulkier than barley meal. Indeed, it is actually less bulky in the dry condition, and after complete soaking in water has only about a 20 % greater bulk than the cereal meal. It is much less bulky than ground sugar-beet pulp, which swells up on soaking to a 43 % greater volume than the potato meal. Potato cossettes and unground sugar-beet pulp are of almost equal bulkiness in the dry condition, but on soaking the latter becomes very much more bulky than the potato cossettes. It is also of interest to note that swelling in all cases was almost complete after soaking the foods for 2 hr. at 37° C., an observation which suggests that very prolonged soaking of meals before feeding to pigs is really not necessary.

DIGESTION TRIALS WITH PIGS

Since potato meal constitutes a more suitable form than potato cossettes for inclusion in pig rations, it was decided to restrict the pig digestion trials to the determination of the digestibility of the potato meal. Two Large White hogs, weighing 140 and 149 lb. respectively at the beginning of the experiment in November 1937, were used for the purpose of the digestion trials. In the first period of feeding, the digestibility of the basal food, composed of 198 g. white fish meal, 660 g. weatings and 924 g. barley meal, was determined. This was followed by a second period in which a reduced amount of the basal diet was supplemented with potato meal, the total weight of the ration being somewhat greater than in the first period on account of the heavier weight of the pigs, which had reached 163 and 166 lb. respectively at the beginning of the second period of feeding. Both pigs were brought very gradually on to the potato meal, the amount of the latter being carefully increased day by day to 700 g., which, with 150 g. white fish meal, 500 g. weatings and 700 g. barley meal, formed the daily ration in the second period. The mean daily consumption of the different foods during the two periods of measurement is shown, on the basis of dry matter, in Tables III and IV. The rations were soaked overnight in water, so as to give a fairly thick slop, and were fed in three approximately equal portions during the day. The animals were allowed drinking water *ad lib.*

The pigs consumed the potato-meal ration very readily. The dung from both animals was of satisfactory consistency, being quite free from the sour smell associated with the faeces from sheep on diets containing the potato products (see later section of this paper). The average moisture content of the faeces in the basal period was 70.7 % (pig 1) and 73.5 % (pig 2), whilst the corresponding figures for the period in which the potato meal was fed were 72.6 % (pig 1) and 75.8 % (pig 2). It will be noted, therefore, that the faeces in the potato-meal period were only slightly moister than in the basal period.

The composition of the potato meal has already been given in Table I. The foods in the basal ration had the following composition (dry matter basis):

	Crude protein %	Ether extract %	N-free extractives %	Crude fibre %	Ash %
White fish meal	70.78	4.80	—	—	24.42
Weatings	18.10	4.87	67.87	5.46	3.70
Barley meal	10.33	2.50	79.00	4.97	3.20

Table III. *Digestibility of basal diet (digestion period 1)*

	Dry matter g.	Organic matter g.	Crude protein g.	Ether extract g.	N-free extractives g.	Crude fibre g.	Ash g.
Pig 1							
Barley meal	795.00	769.56	82.12	19.88	628.05	39.51	25.44
Weatings	574.60	553.34	104.00	27.98	389.99	31.37	21.26
White fish meal	180.20	136.20	127.55	8.65	—	—	44.00
Total consumed	1549.80	1459.10	313.67	56.51	1018.04	70.88	90.70
Total voided	318.25	258.05	47.28	19.02	130.23	61.52	60.20
Total digested	1231.55	1201.05	266.39	37.49	887.81	9.36	30.50
Digestion coefficients, %	79.47	82.31	84.93	66.34	87.21	13.21	33.63
Pig 2							
Barley meal	801.00	775.37	82.74	20.03	632.79	39.81	25.63
Weatings	578.60	557.19	104.72	28.18	392.70	31.59	21.41
White fish meal	180.80	136.65	127.97	8.68	—	—	44.15
Total consumed	1560.40	1469.21	315.43	56.89	1025.49	71.40	91.19
Total voided	316.60	254.86	47.96	17.18	130.57	59.15	61.74
Total digested	1243.80	1214.35	267.47	39.71	894.92	12.25	29.45
Digestion coefficients, %	79.71	82.65	84.80	69.80	87.27	17.16	32.30

Comments on Tables III and IV

The excellent agreement between the digestion coefficients for the two pigs in the basal period of feeding is apparent from the results in Table III.

The potato meal formed about 34 % of the total ration in the second period, and under these conditions the pigs digested the meal with a very high degree of efficiency, the mean digestion coefficients for the dry

matter, organic matter and N-free extractives being 89.4, 89.2 and 96.4 % respectively. The agreement between the values for the two pigs was good, particularly in respect of the N-free extractives.

Table IV. *Digestibility of potato meal (digestion period 2)*

	Dry matter g.	Organic matter g.	Crude protein g.	Ether extract g.	N-free extract- tives g.	Crude fibre g.	Ash g.
Fig 1							
Barley meal	606.80	587.38	62.68	15.17	479.37	30.16	19.42
Weatings	438.30	422.08	79.33	21.35	297.47	23.93	16.22
White fish meal	137.00	103.55	96.97	6.58	—	—	33.45
Potato meal	615.90	591.45	60.11	3.45	513.54	14.35	24.45
Total consumed	1798.00	1704.46	299.09	46.55	1290.38	68.44	93.54
Total voided	300.72	253.82	70.02	16.93	117.30	49.57	46.90
Total digested	1497.28	1450.64	229.07	29.62	1173.08	18.87	46.64
Digested from basal food	939.41	916.18	202.96	28.59	677.48	7.15	23.23
Digested from potato meal	557.87	534.46	26.11	1.03	495.60	11.72	23.41
Digestion coefficients of potato meal, %	90.58	90.37	43.44	29.86	96.51	81.67	95.75
Fig 2							
Barley meal	613.90	594.26	63.42	15.35	484.98	30.51	19.64
Weatings	446.90	430.36	80.89	21.76	303.31	24.40	16.54
White fish meal	137.30	103.77	97.18	6.59	—	—	33.53
Potato meal	616.60	592.12	60.18	3.45	514.12	14.37	24.48
Total consumed	1814.70	1720.51	301.67	47.15	1302.41	69.28	94.19
Total voided	315.60	266.78	75.00	19.17	119.65	52.96	48.82
Total digested	1499.10	1453.73	226.67	27.98	1182.76	16.32	45.37
Digested from basal food	955.17	932.65	204.78	30.50	687.94	9.43	22.52
Digested from potato meal	543.93	521.08	21.89	—	494.82	6.89	22.85
Digestion coefficients of potato meal, %	88.21	88.00	36.37	—	96.25	47.95	93.34
Mean digestion coefficients, %	89.4	89.2	39.9		96.4	64.8	94.5

The potato meal contributed only about 3½ g. of ether extract to the ration, and it is therefore not surprising that it was not possible to secure a reliable determination of the digestion coefficient of this constituent. The large discrepancy between the values for the two pigs for the digestion coefficient of the fibrous component must also be ascribed to the very low percentage of fibre in the potato meal. Many earlier workers, dealing with the problem of the relative digestibility of raw and cooked potatoes, have experienced the same difficulty in securing values for the digestion coefficients of the oil and fibre constituents. It should be emphasized, however, that the most important ingredient of the potato meal is the carbohydrate, and this, as has been shown, is digested to an unusually high degree.

A surprising result of the digestion trials is the lowness of the digestion coefficient of the crude protein of the potato meal (mean value = 39.9 %).

This can scarcely be explained on the grounds of any difficulty in the way of accurate measurement resulting from lowness of the potato protein supply, since the latter formed about 20 % of the total crude protein in the ration. It might have been anticipated that the crude protein of the potato meal would have had a high digestibility, since it contains a high proportion of soluble and easily assimilable "amides" (see Table I). The actual effect, however, of adding the potato meal to the basal diet was to depress the total protein digestibility from 84.9 to 75.8 %.

An explanation of the low value for the digestion coefficient of the potato protein must be sought in the following considerations:

(1) The process of drying the raw potatoes may have depressed the digestibility of the protein constituent. This, however, is scarcely likely, since the drying is carried out slowly at a relatively low temperature. That any such explanation may be excluded was shown by pepsin-HCl determinations *in vitro* of the digestion coefficient of the potato protein, when the high value of 94 % was obtained.

(2) The introduction of the potato meal into the basal diet may have occasioned an increased output of metabolic nitrogenous material in the faeces, which would lead to a lowered apparent digestibility of the protein in the ration. Against this, however, must be set the fact that careful day-to-day inspection of the faeces from both pigs failed to reveal the presence of even small amounts of mucous material.

(3) The inclusion of the potato meal may have caused a speeding-up, such as would be expected with raw potatoes, of the rate of passage of the food through the digestive tract, leading thereby to a less complete digestion of the protein of the food. If this is the correct explanation, it would be expected that a similar depression of the digestibility of the carbohydrate, which was present in much larger amount than the protein, should have been noted. The reverse effect, however, was observed in this case, for the digestion coefficient of the total carbohydrate actually rose from 87.2 to 90.8 % as a result of the introduction of potato meal into the basal diet.

(4) The depression may have been a specific effect of the potato meal, due primarily to its high content of starch. Kellner (1926) has called attention to the depression of protein digestibility that may be caused by a one-sided addition of starch or other digestible carbohydrate to the rations of ruminants or pigs. Any such depression of the digestibility of the protein in the basal ration would, by the method of calculation, be evidenced in the low value that would be obtained for the digestion

coefficient of the potato-meal protein. Investigations carried out in this Institute during recent years have revealed similar depressions of protein digestibility occasioned by the introduction into the rations of pigs of sugar-beet pulp, both plain and molassed, and whole sugar beet, but there is no evidence that the cereals and their products have the same effect as the roots, tubers and their carbohydrate-rich by-products (see Table V).

Whatever the explanation, however, the depression is a real effect. It has been noted by earlier experimenters and, as will be shown later in this paper, was found also to occur with sheep. In a recent summary of work on the nutritive value of potatoes (Woodward *et al.* 1938), the average of a number of determinations of the digestibility of the crude protein in raw, cooked and dried potatoes is given, for pigs, as 58.6 %, the individual values ranging from 26.7 to 84.5 %. For sheep, the mean value works out at 44.3 %, with values ranging from 19.5 to 67.8 %. It is further shown, in work with Shorthorn steers, that the depression was greatest when the dried potatoes were fed with a basal ration containing a protein-rich food like ex. soya bean meal and was not so marked when the basal food consisted merely of hay, a finding that clearly suggests a modification of the digestibility of the basal protein by the presence of the potatoes. In the present trial, therefore, the depression can scarcely be regarded as unexpected, since the basal food contained the protein-rich fish meal.

The digestion coefficients of the potato meal (mean for 2 pigs) are

Table V. *Digestion coefficients, obtained from pig-feeding trials, for potato meal and other carbohydrate-rich foods*

	Organic matter %	Crude protein %	Ether extract %	N-free extrac- tives %	Crude fibre %
Potato meal (1)	89.2	39.9	29.9	96.4	64.8
Barley meal (2)	81.7	81.7	—	88.7	10.8
Maize meal (3)	87.8	80.1	60.5	92.0	35.3
Ground oats (4)	67.5	85.5	86.8	74.3	—
Sussex ground oats (4)	75.9	75.0	84.1	81.2	47.1
Flaked maize (3)	95.4	95.5	44.8	97.1	30.5
Degermed maize meal (cooked) (5)	98.3	94.2	85.0	99.1	94.2
Tapioca flour (6)	97.2	68.5	—	99.0	75.6
Sago pith meal (6)	73.2	—	45.5	85.7	—
Whole sugar beet (7)	91.9	40.0	—	97.1	90.1
Dried sugar-beet pulp (8)	80.2	34.6	—	87.2	84.3
Molassed beet pulp (8)	80.5	24.4	—	89.2	84.4

(1) Present trial.

(2) Wood & Woodman (1924).

(3) Woodman (1925).

(4) Woodman *et al.* (1932).

(5) Woodman & Evans (1932).

(6) Woodman *et al.* (1931).

(7) Woodman *et al.* (1929a).

(8) Woodman *et al.* (1929b).

compared in Table V with corresponding values for a number of carbohydrate-rich and interchangeable feeding stuffs.

Comments on Table V

If the comparison be based on the digestion coefficients of the total organic matter and the N-free extractives, it may be concluded that potato meal, from the standpoint of pig-feeding, is about equal to maize meal, slightly superior to barley meal, and markedly superior to ground oats. This conclusion receives further support from the figures in Table VI showing the amounts of digestible organic matter, per 100 lb. of dry matter, in these feeding stuffs.

Table VI. *Amounts of nutrients digested by pigs from potato meal and other carbohydrate-rich foods per 100 lb. dry matter consumed*

Per 100 lb. of dry matter:	Total organic matter lb.	Crude protein lb.	Ether extract lb.	N-free extractives lb.	Crude fibre lb.
Potato meal	85.95	3.89*	0.17	80.38	1.51
Barley meal	79.91	10.04	—	69.27	0.60
Maize meal	86.09	8.77	3.10	73.42	0.80
Flaked maize	94.39	11.18	0.97	82.02	0.22
Ground oats	65.42	11.03	4.67	49.72	—
Tapioca flour	94.75	1.41	—	91.20	2.14

* On the basis of the digestion coefficient obtained by the *in vitro* method, this figure becomes 9.17 lb.

The main points of distinction between potato meal and the cereals are twofold:

(1) Owing to its non-lignified character, the fibre in potato meal is digested by pigs more efficiently than the fibre in the cereal grains. This superiority is also shared by tapioca flour, whole sugar beet, dried sugar-beet pulp and molassed beet pulp.

(2) The digestibility of the potato-meal protein is low compared with that of the protein in the cereals. It has been shown, however, that this is not due to an inherent lack of digestibility in the potato protein itself, but to a depression of the digestibility of the protein in the ration as a whole, occasioned by the presence of the potato meal. It is incidental to the method of calculating the digestion coefficients that the whole effect of this depression is thrown on to the digestion coefficient of the potato-meal protein.

When using potato meal to replace part of the cereal in pig rations, therefore, it may be necessary to bear in mind that although such replacement will not affect materially the amount of digestible organic matter

in the ration, the amount of digestible protein will thereby be reduced. A ration composed, for example, of 10 % white fish meal, 35 % weatings and 55 % barley meal will contain approximately 14.2 % of digestible crude protein, but if 30 % of the barley meal be replaced by an equal amount of potato meal, the percentage of digestible crude protein in the ration falls to 12.7. This is approximately the percentage that would be present in a ration made up of 6 % white fish meal, 39 % weatings and 55 % barley meal. In order to maintain the percentage at the original level, it would be necessary to increase the white fish meal to about 13 %. Thus, a ration composed of 13 % white fish meal, 32 % weatings, 25 % barley meal and 30 % potato meal would contain about 14.2 % of digestible crude protein.

It should again be emphasized that the present trials were not concerned with any attempts to ascertain the maximum extent to which potato meal may, without possible deleterious effects, replace cereals in the rations of the pig. Nor do the present results enable any conclusions to be drawn respecting the suitability, or otherwise, of this product for inclusion in the rations of *young* pigs. An entirely different experimental technique would be required for the solution of these further aspects of the potato-meal problem. In the strictest sense, the results of these digestion trials are applicable only when the potato meal forms no more than about 34 % of the total rations of pigs of more than 100 lb. live weight.

DIGESTION TRIALS WITH SHEEP

For the purpose of sheep feeding, the coarse potato cossettes constitute a more suitable product than the fine potato meal. It was considered of interest, however, to conduct sheep digestion trials on both forms of artificially dried potatoes, in order to ascertain whether the grinding of the cossettes to a meal leads to any improvement from the standpoint of digestibility. Two wether sheep (Border Leicester \times Cheviot ewe crossed with Suffolk ram) were used in the digestion trials; they were about 10 months old and weighed 126 and 116 lb. respectively at the beginning of the experiments.

The daily ration in period 1 consisted of 500 g. chaffed seeds hay and 800 g. potato cossettes. This was changed in period 2 to 1300 g. of the chaffed seeds hay, whilst in the final period the digestibility of a ration composed of 500 g. chaffed seeds hay and 800 g. potato meal was determined. The composition of the potato cossettes and meal has been given already in Table I. The seeds hay contained, on the basis of dry matter,

12.56 % crude protein, 3.84 % ether extract, 46.31 % N-free extractives, 28.35 % crude fibre and 8.94 % ash.

No difficulty was experienced in securing ready consumption of these rations, but it should be emphasized that, in preliminary periods of feeding, the sheep were carefully accustomed to the potato products, the latter being introduced into the rations in small amounts and then increased gradually to the desired level. The water consumption of the sheep in the potato periods was unusually high, since the potato products were fed in the unsoaked condition. The faeces from both animals were distinctly softer than usual in both potato periods. There was, however, no suggestion of "scouring", the dung being properly "formed" but more lumpy and bulky than when the sheep were subsisting on hay alone. The respective average moisture contents of the faeces in the potato cossettes period, the hay period and the potato meal period were 72.6, 64.0 and 72.1 % (sheep 1) and 71.9, 59.3 and 70.8 % (sheep 2).

In the periods when the potato products were included in the ration, both sheep uniformly gave dung that had a sour smell suggestive of the presence of butyric acid, an indication that starch digestion was not being accomplished wholly by normal enzymatic action, but that a certain proportion of this component was being carried over unchanged into the large intestine, where its digestion was being completed by bacterial agency. This was scarcely surprising, however, since, in consequence of the requirements of the digestion trial, the potato products formed a very high proportion (about 61.5 %) of the total ration. In farm-feeding, when the potato products would be included in the ration in much smaller amount, it is improbable that any such effect on the dung would be noted.

The digestion coefficients (mean for two sheep) of the potato cossettes and the potato meal are recorded in Table VII, in which, for purposes

Table VII. *Digestion coefficients of potato cossettes and potato meal*

	Sheep results		Pig results Potato meal %
	Potato cossettes %	Potato meal %	
Dry matter	80.4	80.9	89.4
Organic matter	81.0	81.4	89.2
Crude protein*	51.0	45.4	39.9
Ether extract	—	—	—
N-free extractives	87.4	88.0	96.4
Crude fibre	—	—	64.8

* By *in vitro* method 94 %.

of comparison, the results obtained for potato meal in the pig digestion trials are also included. The complete figures necessary for the calculation of the digestion coefficients are summarized in the appendix to this paper.

Comments on Table VII

It will be noted that no figures are given for the digestion coefficients of the ether extract and crude fibre, the results in these cases, owing to the very low amounts of these constituents in the potato products, being entirely unreliable.

The following conclusions may be drawn from an inspection of the results in Table VII:

(1) The digestibility of the cossettes is very similar to that of the meal. Grinding of the cossettes to a fine meal does not lead, therefore, to any improvement in the digestibility of the product when used in the feeding of ruminants.

(2) The results from the sheep, in respect of the digestibility of the crude protein in both the cossettes and the meal, resemble those already obtained in the digestion trial with the pigs; namely, the digestion coefficients were very much lower than would have been anticipated on the basis of the high value obtained by the *in vitro* pepsin-HCl determination. The possible causes of this depression have already been discussed in the section dealing with the pig digestion trials. The stimulation of rumen bacterial activity, promoted by the presence of large amounts of potato starch, may conceivably have resulted in a considerably higher utilization of the dietary nitrogen for the synthesis of bacterial protein, with a consequent lowering, possibly because of the presence of anti-enzymes in the bacterial bodies, of the degree to which such nitrogen could be assimilated in the subsequent digestive processes.

(3) Pigs are able to digest the potato meal more efficiently than sheep, this being due to a distinctly higher assimilation of the carbohydrate of the potato product. This is scarcely likely to be a fortuitous finding, nor is it due, in the writers' opinion, to the fact that the sheep rations contained a higher proportion of potato meal than was included in the pig rations. It is in harmony with the results of a number of earlier trials in which the digestibility of raw and of cooked potatoes has been determined in a comparative manner with sheep and pigs (Woodward *et al.* 1938). In these earlier investigations, the average digestion coefficients for the organic matter of the potatoes worked out at 82.6 % for the sheep and 92.8 % for the pigs.

The digestible composition and nutritive value of the potato cossettes

and potato meal are shown in Table VIII. Comparative figures are also given for barley, maize and oats (Wood & Woodman, 1936).

Table VIII. *Digestible composition and nutritive value of potato cossettes and potato meal when fed to ruminants (dry matter basis)*

	Potato cossettes	Potato meal	Barley	Maize	Oats
On the basis of dry matter:	%	%	%	%	%
Digestible crude protein	5.38*	4.43*	8.9	9.1	9.2
Digestible N-free extractives	72.01	73.37	71.6	73.2	51.7
Digestible organic matter	77.70	78.17	84.8	86.3	68.5
Starch equivalent	77.07	77.53	83.9	89.2	68.7
* On basis of <i>in vitro</i> determination of digestibility of crude protein:	9.90	9.17	—	—	—

Comments on Table VIII

A comparison of the figures in Tables VI and VIII re-emphasizes the finding that pigs are able to utilize the dried potato products more efficiently than sheep. Whereas the pigs, per 100 lb. of the dry matter of potato meal, digested 85.95 lb. of organic matter, including 80.38 lb. of N-free extractives, the sheep digested only 78.17 lb. of organic matter, including 73.37 lb. of N-free extractives. As a source of digestible organic matter in the feeding of *pigs*, it has already been shown that potato meal is about equal to maize meal and slightly *superior* to barley meal. It is clear from the figures in Table VIII, however, that from the standpoint of supply of digestible organic matter and starch equivalent in the feeding of *ruminants*, the dried potato products are somewhat *inferior* to barley meal.

This conclusion is, of course, based on the assumption that the moisture contents of the barley meal and the potato products are equal. This, in practice, is not likely to be the case, however. Barley meal usually contains about 14 % of moisture, whereas the potato products are not likely to contain more than about 10 %. If the figures in Table VIII for potato cossettes and barley meal are recalculated on the basis of these moisture contents, it is found that 100 lb. of potato cossettes, containing 10 % of moisture, supplies 69.4 lb. of starch equivalent, including 64.8 lb. of digestible carbohydrate, whilst the corresponding figures for barley meal, containing 14 % of moisture, are 72.1 lb. of starch equivalent, including 61.6 lb. of digestible carbohydrate. Bearing in mind that the value for the starch equivalent of the potato cossettes takes no account of the contribution of the small amounts of ether extract and crude fibre in this product, it is not unreasonable to assume

that, in feeding practice, potato cossettes (or meal) should be capable of replacing barley meal, lb. for lb., in the rations of sheep and cattle.

When making such replacement, however, it must be borne in mind that the potato products exert a depressing effect on the digestibility of the protein of the ration in which they are included. On the basis of the *in vitro* determinations of protein digestibility, potato cossettes should contain 9.90 % of digestible crude protein; the actual figure, as determined by sheep experiments, was only 5.38 %. The mean value for both the cossettes and the meal was 4.9 % (dry matter basis), a figure very similar to that for the mean percentage of "amides", namely, 4.75 % (see Table I). From what has been written, however, it should not be inferred from this comparison that the digestible fraction of the potato crude protein consists almost wholly of "amides", even though it is customary to assume that the "amides" of a food are completely assimilable. It would manifestly be unsafe to attempt to calculate, from the available data, a value for the protein equivalent of the potato products, and indeed, when the whole of the factors involved in this question are given due consideration, it is probable that the digestible crude protein, as determined in this investigation, affords the best basis for assessing the contribution of the potato products to the digestible protein content of the ration.

CONCLUSIONS

The main conclusions from this investigation, in which the composition and digestibility, when fed to pigs and sheep, of potato cossettes and potato meal have been determined, may be summarized briefly as follows:

Pigs, subsisting on a ration containing about 34 % of potato meal, digested the potato product with a very high degree of efficiency, the digestion coefficients for the dry matter, organic matter and N-free extractives being 89.4, 89.2 and 96.4 % respectively. If comparisons be based on the digestion of total organic matter, it may be concluded that potato meal, from the standpoint of pig-feeding, is about equal to maize meal, slightly superior to barley meal and markedly superior to ground oats. Per 100 lb. of dry matter consumed, potato meal furnishes the pig with 86.0 lb., maize meal with 86.1 lb., barley meal with 79.9 lb. and ground oats with 65.4 lb. of digestible organic matter.

The digestibility of potato meal protein in the pig is low compared with that of the protein in cereals. It has been shown, however, that this

is not due to an inherent lack of digestibility in the potato protein itself, but to a depression of the digestibility of the protein in the ration as a whole, occasioned by the presence of the potato meal. It is incidental to the method of calculating the digestion coefficients that the whole effect of this depression is thrown on to the digestion coefficient of the potato-meal protein.

When using potato meal to replace part of the cereal in pig rations, therefore, it may be necessary to bear in mind that although such replacement will not affect materially the amount of digestible organic matter in the ration, the amount of digestible protein will thereby be reduced. In order to maintain the percentage at the original level, it will be necessary to increase the allowance of protein-rich food in the ration. Thus, a ration composed of 10 % white fish meal, 35 % weatings and 55 % barley meal contains approximately the same amount of digestible crude protein, namely, about 14.2 %, as one made up of 13 % white fish meal, 32 % weatings, 25 % barley meal and 30 % potato meal.

Pigs are able to utilize the dried potato products more efficiently than sheep. Whereas the pigs, per 100 lb. of the dry matter of potato meal, digested 86.0 lb. of organic matter, including 80.4 lb. of N-free extractives, the sheep digested only 78.2 lb. of organic matter, including 73.4 lb. of N-free extractives. From the standpoint of supply of digestible organic matter and starch equivalent in the feeding of ruminants, the dried potato products are somewhat inferior to barley meal, if the comparison be based on the assumption that the potato products and the barley meal have equal moisture contents. If, however, as is more likely to be the case in feeding practice, the barley meal contains about 14 % of moisture and the potato products only about 10 %, it is shown that the latter should be capable of replacing barley meal, lb. for lb., in the rations of sheep and cattle. As in the case of pig-feeding, allowance should be made, when making such replacement, for the fact that the potato products exert a depressing effect on the digestibility of the protein of the ration in which they are included.

It was found in the sheep digestion trials that the digestibility of the cossettes is very similar to that of the potato meal. Grinding of the cossettes to a fine meal does not lead, therefore, to any improvement in the digestibility of the product when used in the feeding of ruminants.

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APPENDIX. SHEEP DIGESTION TABLES*

Sheep 1

	Dry matter g.	Organic matter g.	Crude protein g.	Ether extract g.	N-free extrac- tives g.	Crude fibre g.	Ash g.	Dry matter g.	Organic matter g.	Crude protein g.	Ether extract g.	N-free extrac- tives g.	Crude fibre g.	Ash g.
	Period 1. (800 g. potato cosettes + 500 g. chaffed seeds hay)													
Hay supply	440.00	400.66	55.26	16.90	203.76	134.74	39.34	440.00	400.66	55.26	16.90	203.76	124.74	39.34
Hay residues	21.30	17.89	3.27	0.82	9.50	4.30	3.41	142.80	129.32	17.21	5.94	64.37	41.80	13.48
Hay consumed	418.70	382.77	51.99	16.08	194.26	120.44	35.93	297.20	271.34	38.05	10.96	139.39	82.94	25.86
Potato cosettes	713.40	684.29	75.19	4.49	587.77	16.84	29.11	713.40	684.29	75.19	4.49	587.77	16.84	29.11
Total consumed	1132.10	1067.06	127.18	20.57	782.03	137.28	65.04	1010.60	955.63	113.24	15.45	727.16	99.78	54.97
Total voided	339.49	298.51	67.50	8.16	146.51	76.34	30.98	292.50	266.11	61.51	8.13	135.51	60.96	26.39
Total digested	802.61	768.55	59.68	12.41	635.52	60.94	34.06	718.10	689.52	51.73	7.32	591.65	38.82	28.58
Digested from hay	223.42	208.60	20.68	11.93	116.61	59.38	14.82	149.72	141.63	14.12	7.14	83.65	36.72	8.09
Digested from cosettes	579.19	559.95	39.00	0.48	518.91	1.56	19.24	568.38	547.89	37.61	0.18	508.00	2.10	20.49
Digestion coefficients of cosettes, %	81.19	81.83	51.87	10.69	88.28	9.27	66.09	79.67	80.07	50.02	4.01	86.43	12.47	70.39

Period 2 (1300 g. chaffed seeds hay)

Hay supply	1170.00	1065.41	146.95	44.93	541.83	331.70	104.59	1170.00	1065.41	146.95	44.93	541.83	331.70	104.59
Hay residues	68.10	57.52	9.46	2.70	28.42	16.94	10.58	234.80	211.74	24.51	10.03	105.12	72.08	23.06
Hay consumed	1101.90	1007.89	137.49	42.23	513.41	314.76	94.01	935.20	853.67	122.44	34.90	436.71	259.62	81.53
Total voided	513.73	458.50	82.81	10.89	205.23	159.57	53.23	464.52	408.49	77.00	12.15	174.64	144.70	58.03
Total digested	588.17	549.39	54.68	31.34	308.18	155.19	38.78	470.68	445.18	45.44	22.75	262.07	114.92	25.50
Digestion coefficients of hay, %	53.38	54.51	39.77	74.21	60.03	49.30	41.25	50.33	52.15	37.11	65.19	60.01	44.27	31.28

Period 3 (800 g. potato meal + 500 g. chaffed seeds hay)

Hay supply	452.50	412.05	56.83	17.38	209.56	128.28	40.45	452.50	412.05	56.83	17.38	209.56	128.28	40.45
Hay residues	—	—	—	—	—	—	—	10.00	8.87	1.01	0.27	5.06	2.53	1.13
Hay consumed	452.50	412.05	56.83	17.38	209.56	128.28	40.45	442.50	403.18	55.82	17.11	204.50	125.75	39.32
Potato meal	703.80	675.86	68.69	3.94	586.83	16.40	27.94	703.80	675.86	68.69	3.94	586.83	16.40	27.94
Total consumed	1156.30	1087.91	125.52	21.32	796.39	144.68	68.39	1146.30	1079.04	124.51	21.05	791.33	142.15	67.26
Total voided	336.00	302.43	69.40	8.96	130.65	73.42	33.57	364.50	329.84	74.94	10.61	135.42	88.87	34.66
Total digested	820.30	785.48	56.12	12.36	665.74	71.26	34.82	781.80	749.20	49.57	10.44	635.91	53.28	32.60
Digested from hay	241.23	224.54	22.60	12.90	125.80	63.24	16.69	222.55	210.25	20.71	11.15	122.72	55.67	12.30
Digested from potato meal	579.07	560.94	33.52	—	519.94	8.02	18.13	559.25	538.95	28.86	—	513.19	—	20.30
Digestion coefficients of meal, %	82.28	83.00	48.80	—	88.60	48.90	64.89	79.46	79.74	42.02	—	87.45	—	72.66

* The pig digestion tables are given in the text of the paper.

Note. The care of the experimental animals was in the hands of Messrs V. Thurlbourn and C. Bendall.

THE RESPONSE OF PERMANENT GRASSLAND TO NITROGEN AND THE EFFICIENCY OF ITS RECOVERY

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(With One Text-figure)

INTRODUCTION

EXPERIMENTS on the use of nitrogenous fertilizers on permanent grass were started at the Hertfordshire Institute of Agriculture in 1927 and have continued since. For the first four years they were in connexion with the "new" system of rotational grazing which was being advocated at that time. Results were described and summarized in two papers in this *Journal* (Gardner *et al.* 1929, 1931). They were obtained on large 5-acre plots for which no estimates of error, other than the sampling error, could be calculated, and it was clear that the comparatively small response to 3 cwt. sulphate of ammonia per annum per acre (between 20 and 30 % increase over the no-nitrogen plots) needed adequate replication for its accurate measurement. Owing to the limited time and facilities available, this entailed the use of small plots and cutting the produce, with the consequent departure from true grazing conditions. However, by the use of a fresh area every year, it was hoped that the results would have some bearing on practice. For the first cut of each year the yields represent exactly what would be present on similar grassland rested throughout the winter after being closely grazed in October. The three succeeding cuts become more and more removed from grazing conditions, but nevertheless provide information on such points as the effect of nitrogen on clover development, recovery of nitrogen, and the growth available for artificial drying.

TYPE OF SOIL AND GRASS

The soil concerned in the experiments is a moderately heavy loam shown on the "Drift" map as Boulder Clay. For some years it has been liberally treated with phosphates and potash and, occasionally, lime. It has a high percentage of exchangeable calcium, but is still not neutral,

the pH being about 6. The land has been down to grass for over a hundred years, but earlier still, as shown by the still persisting ridges and furrows, was under the plough.

The composition of the herbage was fully described in the second of the two earlier papers. *Lolium perenne* is the dominant species, *Agrostis* spp. come second, *Festuca ovina* third, and *Poa* spp. fourth. Wild white clover is very variable in amount both from place to place and from year to year. Herbs and weeds are low in amount, *Achillea millefolium* and *Ranunculus bulbosus* being perhaps the chief.

METHODS

Each autumn as uniform an area as possible was selected on grass used for grazing during the preceding months of the year. This was trimmed with shears, rolled and fenced in. On it a 5 × 5 Latin square, each plot 4 sq. yd. in area, was marked out with small cane pegs: to ensure an adequate supply of phosphate and potash, superphosphate and sulphate of potash were applied evenly during the winter. First dressings of nitrogen fertilizers were applied during the first week of February, and the "early bite" was cut within a day or two of 20 April in each of the six years to be described. The three subsequent cuts were in May, July, September or early October.

For some years ordinary garden shears were used for cutting, but later a "Rotoscythe" 18 in. mower was utilized and found admirable for the purpose. Owing, however, to the mangling of the grass by the propeller blade it was found necessary to cut a sample with shears from each of the plots just before mowing it; these samples, when bulked for treatments, provided material for dry matter and nitrogen determinations, and for subdivision into "grasses", "clovers", "weeds" (=other species) and "waste" (soil, dried-up grass, etc.). It was not possible to effect this separation for each of the twenty-five plots, but various tests, when the method was first devised ten years ago, showed that the bulking of replicates and the extraction of a small subsample for the separation could be carried out with considerable accuracy.

Using the Rotoscythe (and shears for sampling), two persons working systematically can sample, cut, and weigh the twenty-five plots in about 2 hr.: with shears it required three men working hard for 3 hr.

By these simple methods it has been possible to measure the effect of nitrogen dressings in different forms and amounts on the April "early bite", their influence on the proportion of grasses and clovers later in

the year, the comparative yields obtained by applying all the dressing early or splitting it into an early and a later application, the percentage recovery of the nitrogen applied, the reason for the extraordinary variation of this percentage, and the effect of the nitrogen on the crude protein (or nitrogen) content of "grasses", "clovers", "weeds", as well as of the complete herbage. From the latter figures a little circumstantial evidence can be extracted in favour of Virtanen's theory of the excretion of nitrogen compounds by clovers.

EXPERIMENTAL ERRORS

With such small plots and the possibility of patches arising from the excreta of animals grazing during the preceding months, high errors might have been anticipated. Actually they were low. For the year's production, standard errors for the mean of five plots were in successive years 1.76, 4.1, 2.35, 2.16, 3.3, 3.34% of the general mean, or in cwt. per acre 0.74, 1.60, 1.36, 1.43, 2.13, 1.43. For the "early bite", when irregularities show their maximum effect, the corresponding figures were 4.8, 5.95, 4.9, 6.35, 5.6, 3.25% or 0.50, 0.45, 0.76, 0.42, 0.67, 0.46 cwt. per acre.

RESULTS

Value of nitrogen for "early bite"

The results for six years are given in Fig. 1. Fertilizers were applied during the first week of February, and the herbage was cut within a day or two of 20 April in each year.

Yields on the nil plots varied from 4.1 cwt. dry matter per acre in 1934 to 12.1 cwt. in 1935, a difference which is possibly due to the higher soil temperature in March of the latter year (av. temp. 1 ft. in ground 40.2 and 42.4° F., respectively).

One treatment, 3 cwt. sulphate of ammonia per acre, was constant throughout. The *extra* dry matter in April produced by this treatment in successive years has been 7.84, 6.64, 5.68, 2.11, 5.19, 8.75 cwt. per acre, an average of 6.05 or 2.02 cwt. dry matter per cwt. fertilizer. The low figure of 2.11 in 1936 was a result of applying the fertilizers under unsuitable weather conditions (the grass was damp, and frost followed, causing severe scorching). This was the only occasion in a long series of experiments where this effect was experienced, and only the desire to adhere to the prearranged time of application led to this exception. Omitting 1936, the average rises to 6.8, or 2.3 cwt. dry matter containing 21.7% protein per cwt. sulphate of ammonia applied.

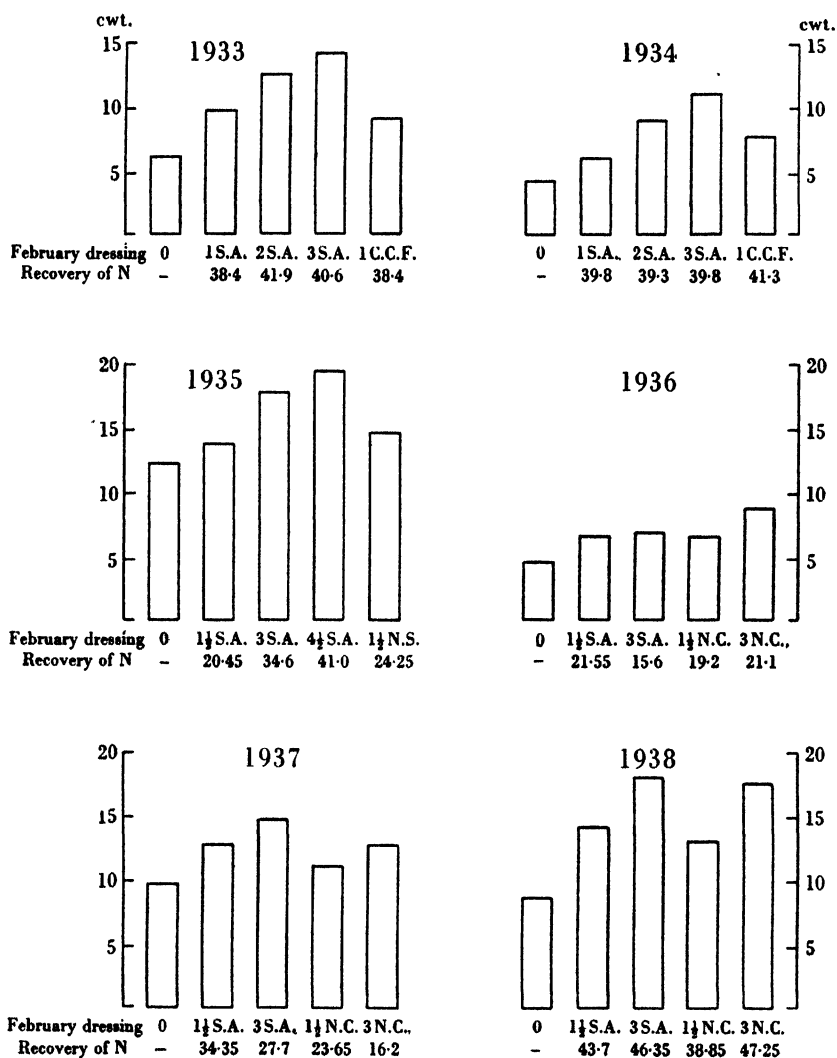


Fig. 1. Production of early bite in cwt. dry matter per acre and percentage recovery of applied nitrogen.

Note. S.A.=sulphate of ammonia; N.C.=nitro-chalk; N.S.=nitrate of soda; C.C.F.=concentrated complete fertilizer No. 4, containing N 10.4 %, P_2O_5 20.8 %, K_2O 10.4 %. The figure preceding S.A. in this figure and throughout the general text=cwt. per acre. For other fertilizers the figure denotes cwt. S.A. to which they are equivalent in nitrogen.

Fig. 1 shows very clearly the proportionality between response and rate of application. In 1935, when one treatment was a February application of 4.5 cwt. sulphate of ammonia per acre, there was no appreciable falling off in response, and the efficiency of recovery of the nitrogen was more than maintained for this dressing. These results justify the suggestion that if "early bite" is to be forced it is better to use a heavy dose of nitrogen on a small area since the longer growth will be more readily grazed. Further, the probable detrimental effects of clover suppression later in the year will be limited to the smaller area.

The comparative value of different fertilizers for early bite can also be seen in Fig. 1. Only in one year, viz. 1937, did the difference between forms of nitrogen reach the 5% level of significance, when sulphate of ammonia at two levels was superior to nitro-chalk, at equivalent levels. Taking the whole series of experiments it seems probable that ammonia nitrogen is slightly superior to nitrate nitrogen for early grass. In 1933 and 1934 there was no evidence of any advantage from the use of the concentrated complete fertilizer in which nitrogen is present as ammonium phosphate.

Recovery in April and May of the nitrogen applied in February

For the first (April) cut the percentage recovery figures are included in Fig. 1. The second cut was taken during the third week in May, i.e. a month after the first cut. Averaging levels and kinds of nitrogen the results for successive years are:

Percentage recovery of nitrogen in first two cuts

	1933	1934	1935	1936	1937	1938
April	39.4	40.0	30.8	19.4	25.5	44.0
May	3.2	22.0	1.6	- 2.4	6.1	10.0
Total	42.6	62.0	32.4	17.0	31.6	54.0

The low figure for 1936 has already been explained as due to scorching. Omitting this, the average recovery of the nitrogen applied in February was 35.9% in April with a further 8.6% in May, a total of 44.5%. It is thus evident that one of the most efficient uses of nitrogen is for the production of early bite on suitable grassland.

Reference to Fig. 1 shows that, up to a level of 4.5 cwt. sulphate of ammonia per acre, there is no falling off in efficiency of recovery: actually in 1935, when this heavy dressing was included, the return was 41.0% for the first cut and 48.2% for the first two cuts, both of which figures are above those for the lighter dressings.

Comparing forms of nitrogen, it seems that sulphate of ammonia was recovered slightly more efficiently than ammonium phosphate (in concentrated complete fertilizer) and was equal or slightly superior to nitro-chalk. It was compared only once in this series with nitrate of soda, and was then slightly inferior. (In another series of experiments these two were compared over several years; they were then equally efficient for early grass but for autumn grass nitrate nitrogen was distinctly superior.)

Growth in May

When moisture and temperature conditions are not far from average the rate of growth of grass in May is very high. The April cut, representing growth since the previous autumn, averaged 7.5 cwt. dry matter on the nil plots: the May cut, measuring almost exactly one month's growth, averaged 10.4, i.e. 50% more than for the previous six months. The seasonal range of variation in May was similar to that in April.

As can be seen from the nitrogen recovery figures of the previous section, the February dressing usually shows in May, but, except in 1934, the effect has been comparatively small. The differences between nil and 3 cwt. of sulphate of ammonia were 0.8, 5.43, 2.24, 2.68, 1.63, 2.46 cwt. dry matter per acre with an average of 2.54 which may be compared with 6.1 for April. It can be assumed that by the end of May the early dressing of nitrogen has, normally, been fully used. One qualification needs to be attached to this statement: if there is anything of the nature of a cycle, including a locking-up stage, in the utilization of applied nitrogen, it could come into action again later in the year. On two or three occasions effects of this kind have been detected in the yields of dry matter. Thus, in the fourth cut of 1938, the difference between nil and 3 cwt. of sulphate of ammonia all applied early was 1.08 cwt. with a standard error of 0.41, so that it reaches significance at the 2% point. A single example would not carry much weight, since in a series of experiments such differences would occur occasionally by chance, but one very clear instance of the same kind was observed on a big scale in the autumn of 1936 on a neighbouring farm where it was known that nitrogen had not been applied since the spring. In this case the colour effect was so marked as to suggest an application of nitrate a week or so previously.

Growth in June onwards

Certain of the plots which had a smaller dose of fertilizer in February received another equal dressing after the May cut. In measuring the

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effect of this it has been assumed that the earlier dose was exhausted or negligible in its influence.

The June–July growth (approximately two months) represented by the third cut was extremely variable, ranging from 5.90 cwt. in 1934 to 28.65 cwt. in 1937 on the nil plots. This wide range is mainly a rainfall effect, the growth apparently being controlled chiefly by the May rainfall. This was 0.6 in. in the former year and 2.78 in. in the latter: in June and July the rainfall difference was small.

The August–September growth, measured by the fourth cut, was not so variable, ranging from 8.08 cwt. in 1933 to 21.39 cwt. in 1936 with an average of 24.4 cwt. These two months, therefore, are as productive as May.

The responses to nitrogen in the second half of the season were as follows (omitting 1933 when the second dose was not applied until after the third cut:

				1934	1935	1936	1937	1938	Average per cwt. s.a.
Amount of s.a.	1	1½	1½	1½	1½	
Extra dry matter:	July	0.90	4.14	2.41	5.25	5.51	2.60
	Sept.–Oct.	1.26	– 0.62	– 1.36	1.20	2.51	0.43
	Total	2.16	3.52	1.05	6.45	8.02	3.03

The 2.6 cwt. dry matter may be compared with 2.03 per cwt. sulphate of ammonia for the early bite and the 0.43 with 0.85 for May: in dry matter the total response was therefore about the same but since the periods of growth were different this comparison is hardly a fair one.

Recovery of nitrogen applied in June

When the percentage recovery is calculated from the yield and analysis of the herbage the figures are:

	1934	1935	1936	1937	1938
July	24.2	8.3	– 18.4	– 18.4	37.3
Sept.–Oct.	16.2	– 19.0	– 37.0	– 8.4	18.5
Total	40.4	– 10.7	– 55.4	– 26.8	55.8

These figures show that, although in production of dry matter the nitrogen applied in June can be as effective as the February dressing, yet its efficiency of recovery may be extraordinarily low. The explanation of this lies in the effect of nitrogen on clover production. The subdivision of the herbage for each treatment on each occasion of cutting into “grasses”, “clovers”, “weeds” and “waste” enables the weight per acre of these groups to be calculated. Details are not given but the

following averages are extracted for the six years. All figures are cwt. per acre.

	Av. wt. of herbage on nil plots	Av. wt. of clovers on nil plots	Av. wt. of clovers on 3 s.a. plots	Depression due to 3 s.a.
April	7.5	0.28	0.22	0.06
May	10.4	1.21	0.58	0.63
July	17.4	4.02	2.17	1.85
Sept.-Oct.	12.3	3.21	2.12	1.09

In April the amount of clovers averaged only 0.28 cwt. per acre on the no-nitrogen plots, and the depression is the trivial amount of 0.06 cwt. In May the depression is ten times as great but is still comparatively small; in July it has trebled again and now represents the substantial amount of 1.85 cwt. per acre (equal to about 9 cwt. before drying); in September it fell to a little over a cwt. per acre.

The range of the July depression in different years has been from 0.4 to 3.87 cwt. In the case of the low figure, 0.4, it would be easy for the June applied nitrogen to produce a sufficiently great increase in "grasses" to give an efficient recovery, but for the high figure it would obviously be necessary for an unusual response in grass production to take place in order to give a positive recovery, particularly as clovers have a higher protein content than other species. Only in a year, or on a sward, of low clover development were high recoveries of applied nitrogen maintained throughout the year. An outstanding example of this was 1938 when the *total* clover for the year on the nil plots was only 1.42 cwt. per acre as against 16.69 cwt. in 1937. In 1938 the recovery of the February dose of 1.5 cwt. sulphate of ammonia was 57.4% and of a similar dose in June 55.8%—practically equal figures. As a contrast with this, the *depression* of clovers in 1936 was 6.47 cwt. per acre, and the "recovery" of the second dressing of sulphate of ammonia was -55.4%.

These examples show very clearly the necessity for specifying the kind of sward to which the nitrogen is applied whenever attempting to measure the efficiency of uptake of the dressing.

Examining the 1936 results more closely and using the figures for "grasses" on the nil plots and on the plots which received a total dressing of 3 s.a. in two doses, the results for the second dose are:

	Grasses on nil plots		Grasses on nitrogen plots	
	Dry matter cwt. p.a.	Crude protein cwt. p.a.	Dry matter cwt. p.a.	Crude protein cwt. p.a.
3rd cut	17.14	2.77	21.70	3.27
4th cut	9.31	1.64	10.09	1.67
Total	26.45	4.41	31.79	4.94

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The 0.53 extra cwt. of crude protein in the 5.34 extra cwt. of "grasses" correspond to a recovery of +27.4% of the nitrogen applied before the third cut as against the apparent recovery, calculated from the total herbage, of -55.4%. However, even when allowance is thus made for clover depression, 1936 stands out as a year of low recoveries which may, perhaps, be attributed to the abnormally high rainfall.

Total production for the year

The total dry matter on the no-nitrogen plots and the plots which received sulphate of ammonia at the rate of 3 cwt. per acre, total clover production, total crude protein, and total recovery of nitrogen, are given in Table I.

Table I. *Total production in cwt. per acre for the year*

	1933	1934	1935	1936	1937	1938	Average
Dry matter							
Nil plots	38.58	31.80	54.91	64.36	63.63	32.48	47.63
3 s.a.	45.87	44.24	56.05	64.83	70.93	45.78	54.63
Difference	7.29	12.46	1.14	0.47	7.30	13.30	7.00
Clover							
Nil plots	3.56	3.88	8.26	18.35	16.685	1.52	8.71
3 s.a.	1.455	1.14	2.60	11.88	14.10	0.52	5.28
Difference	-2.105	-2.74	-5.66	-6.47	-2.585	-1.00	3.43
Crude protein							
Nil plots	5.68	4.98	8.80	12.13	9.88	4.26	—
3 s.a.	7.11	7.56	8.69	11.18	10.61	6.77	—
Difference	1.43	2.58	-0.11	-0.95	0.73	2.51	—
% recovery of nitrogen	37.0	66.9	-2.8	-24.5	19.1	65.1	—

Since the figures for the recovery of nitrogen at different times of the season and reasons for their variation have been discussed, it is only necessary to point out that the net recovery per annum has varied from +66.9% in 1934 to -24.5% in 1936, which was the season of highest clover production and highest depression by nitrogen.

Relationship between dry matter and rainfall

Using rainfall for harvest years (Oct.-Sept.) the following figures show the very regular correspondence between rainfall and total yield on the no-nitrogen plots.

	1933	1934	1935	1936	1937	1938	Average
Rainfall, in.	20.56	16.00	27.55	34.19	32.19	17.82	24.74
Nil plots, cwt. per acre	38.58	31.80	54.91	64.36	63.63	32.48	47.63
Dry matter per inch of rain	1.88	1.99	1.99	1.88	1.98	1.82	1.92

The dry matter per inch of rain averaged just under 2 cwt. and varied remarkably little from this in any of the six years.

*Effect on total production of 3 cwt. sulphate of ammonia
applied in February*

For this dressing, which has been one of the treatments each year, the exceptionally low response in 1936 has already been discussed, but apart from this the returns in cwt. dry matter per acre range from 1.14 to 14.09 cwt. The two highest returns were in the years of *lowest* rainfall, bearing out an observation previously recorded (Gardner *et al.* 1931). This is an interesting example of a favourable factor, namely, additional plant food, tending to make up for an unfavourable factor limiting growth, namely, low rainfall.

Part of the variation in response is accounted for by the depression of clovers on the nitrogen plots. As shown in Table 1 this *depression* was greatest in the years of lowest response to nitrogen (as measured by increase in total herbage), i.e. in years of highest rainfall and greatest production. It is legitimate, therefore, to conclude that the depression is mainly a question of competition; when production of herbage is low, competition is low and there is room for nitrogen to produce its maximum effect on non-leguminous species. When, owing to a "good growing season", productivity is high, competition between clovers and non-legumes is severe and is intensified by the application of nitrogen. Since there must be a limit to the amount of dry matter which can be produced on an acre of turf, when this limit is approached any factor tending to increase the grasses might be expected to act against legumes, the total herbage tending to remain constant.

(On the particular grassland used for these experiments the limit of dry matter production appears to be about 75 cwt. per acre for the method of management employed, i.e. cutting four times per annum.)

Comparative effect on total production of different forms of nitrogen

In 1933 and 1934 nitrogen as sulphate of ammonia was compared with nitrogen as ammonium phosphate (in the concentrated complete fertilizer). For the year's production comparative figures, in cwt. per acre dry matter, were as follows:

	S.A.	Equiv. C.C.F.	Difference	S.E. of difference
1933	41.91	40.39	1.52	1.05
1934	39.58	38.82	0.76	2.26

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The differences are in favour of sulphate of ammonia, but are below the 5% level of significance.

In 1936, 1937, 1938, the experiment was uniformly conducted with a comparison between single and split doses of sulphate of ammonia and nitro-chalk, the results being:

	1936		1937		1938	
	Split	Single	Split	Single	Split	Single
S.A.	68.35	64.83	73.58	70.93	48.28	45.78
N.C.	67.19	66.52	69.35	66.74	42.99	43.27
Difference	1.16	-1.69	4.23	4.19	5.29	2.51
Mean difference S.A.-N.C.	-0.26		4.21		3.90	
Standard error of difference	1.43		2.13		1.43	

Taking into account that in 1936 the sulphate of ammonia was applied under conditions leading to scorching it can be concluded that this form is more effective than nitro-chalk, reaching significance at about the 2% point in 1938 and just failing to reach the 5% point in 1937.

Comparison between a single full application of sulphate of ammonia in February and two half-doses in February and June

This comparison has been made in each of the six years: the chief results are given in Table II in which only differences are tabulated.

Table II. *Difference between a single full and two half-doses of S.A.*

	In total yield of herbage cwt. per acre	In efficiency of recovery of nitrogen %	In amount of clovers cwt. per acre
1933	1.88	4.6	-0.26
1934	1.72	8.4	0.16
1935	-4.25	-6.8	-2.04
1936	-5.52	-6.0	0.84
1937	-2.65	10.1	1.38
1938	-1.71	8.5	0.27
Average	-1.75	3.3	0.06

On the average the weight of dry matter is in favour of the split dose, but since the recovery slightly favours the single early application the yield difference may be chiefly a result of cutting at a later stage of development. The effect on growth of clovers is, on the average, practically the same. No reason can be suggested for the exceptionally low clover development on the "single-early" plots in 1935.

Effect of sulphate of ammonia on the non-leguminous herbage

The figures of Table III show the effect of nitrogen on "grasses" and "weeds" (=other non-leguminous species).

Table III. "Grasses" and "Weeds". Cwt. dry weight per acre

	1933		1934		1935		1936		1937		1938	
	Grass	Weeds	Grass	Weeds	Grass	Weeds	Grass	Weeds	Grass	Weeds	Grass	Weeds
3 cwt. s.a.	35.38	2.71	34.76	2.13	50.25	0.94	45.61	3.54	49.85	1.17	41.91	1.40
Nil	24.11	2.46	20.18	2.66	41.39	3.01	41.27	2.33	38.91	2.27	26.85	1.68
Difference	11.27	0.25	14.58	-0.53	8.86	-2.07	4.34	1.21	10.94	-1.10	15.06	-0.28
Total difference	11.52		14.05		6.79		5.55		9.84		14.78	
Rainfall	20.45		18.60		27.55		34.30		32.19		17.82	

Here the high response in years of low rainfall as contrasted with the low response in years of high rainfall is still more clearly shown. For the three years with rainfall below 21 in. the extra weight of grasses plus weeds averaged 13.45 cwt. and for the other three years 7.4 cwt.

Effect of nitrogen on the crude protein content of the separated grasses

The discussion is again restricted to the plots not receiving nitrogen and those receiving 3 cwt. of sulphate of ammonia during the first week of February, the results being given in Table IV.

Table IV. Percentage crude protein in "grasses"

	1933				1931				1935			
Cut no. . .	1	2	3	4	1	2	3	4	1	2	3	4
With 3 cwt. s.a.	17.08	15.17	13.29	22.05	24.63	15.74	15.92	16.68	19.02	14.16	12.66	17.81
No N	16.49	14.77	14.02	22.15	19.76	15.96	15.38	16.60	16.10	14.56	12.82	19.40
Difference	1.49	0.40	-0.73	-0.10	4.87	-0.22	0.54	0.08	2.92	-0.10	-0.16	-1.59

	1936				1937				1938			
Cut no. . .	1	2	3	4	1	2	3	4	1	2	3	4
With 3 cwt. s.a.	20.67	14.90	15.10	16.92	16.56	15.77	10.44	15.60	17.64	17.47	11.56	13.42
No N	17.39	16.00	16.18	17.62	14.38	14.96	13.62	15.20	14.48	15.62	10.55	13.09
Difference	3.28	-1.10	-1.08	-0.70	2.18	0.81	-3.18	0.40	3.16	1.85	1.01	0.33

Averages for cuts				
Cut no. . .	1	2	3	4
With 3 cwt. s.a.	19.42	15.58	13.16	17.08
No N	16.43	15.31	13.76	17.34
Difference	2.99	0.27	-0.60	-0.26

For the first (April) cut the crude protein content of the grasses is considerably increased by the February nitrogen, being on the average 19.42 as against 16.43 on the nil plots.

For the second (May) cut the difference is sometimes positive and sometimes negative, averaging 0.27 for the six years. This conforms with

the conclusion given earlier that by May the direct effect of the February nitrogen has almost disappeared.

For the third and fourth cuts the differences are also sometimes positive and sometimes negative and are so variable that at first sight, no regularity can be detected. But, on comparing them with the depression of clovers on the nitrogen plots, a correlation is at once apparent. In Table V the excess protein *percentage* in the grasses of the *nil* plots is tabulated against the extra weight of clovers on these plots.

Table V. *Third and fourth cuts. Relation between protein content of "grasses" and amount of clovers*

	Weight of clovers Nil-3 cwt. s.a.		% crude protein in grasses Nil-3 cwt. s.a.	
	Third cut	Fourth cut	Third cut	Fourth cut
1933	1.01	0.36	0.73	0.10
1934	0.79	1.15	-0.54	-0.08
1935	2.87	2.19	0.16	1.59
1936	2.16	2.555	1.08	0.70
1937	3.87	-1.40	3.18	-0.40
1938	0.40	0.31	-1.01	-0.33
Average		1.36		0.43

The correlation coefficient for the twelve pairs of protein differences and the corresponding clover differences is 0.765 which is highly significant. Since for the first cut (when the amount of clover is negligible) grasses from the nitrogen treated plots are invariably richer in protein than those from the nil plots, it may be argued that a higher protein content is evidence of more available nitrogen in the soil. For the third and fourth cuts it is, on the average, the grasses of the nil plots which are richer in protein to a degree which is significantly correlated with the excess of clovers on these plots. This may be regarded as at least circumstantial evidence in support of Virtane's theory of the excretion of available nitrogen compounds from the roots of leguminous plants.

Effect of nitrogen on the crude protein content of clovers

It is a matter of interest whether the applied nitrogen raises the protein content of clover species as it does of grass species. The results of using figures for the first cut in each of the six seasons are shown in the following table.

In each year the clover from the nitrogen plots has a considerably higher crude protein content, the average difference being 2.95, or omitting the high figure for 1935, 2.55. It seems therefore that a

Crude protein of clovers

	From 3 cwt. S.A. plots	From nil plots	Difference
1933	28.75	26.14	2.61
1934	31.27	28.15	3.12
1935	29.16	24.20	4.96
1936	28.60*	26.80	1.80
1937	24.25	21.55	2.70
1938	26.60	24.08	2.52

* Figure for nitro-chalk plots used as clover from 3 S.A. plots was very small in amount and gave the exceptionally high figure of 36.35.

considerable amount of applied nitrogen can be taken up by the clovers at least in the early part of the season.

In another series of experiments for which twenty-five comparisons are available between clovers from nitrogen and from no nitrogen plots, the samples being from month old herbage at varying times of the year, the average crude protein contents were 26.92% and 26.42%.

The increase due to the added nitrogen was 0.50 with a standard error of 0.22 and must be regarded as significant.

*Relative importance of clovers to total herbage
at different seasons of the year*

Averaging the figures for the successive cuts over the six years of experiment the results were, for the no-nitrogen plots:

	Total herbage cwt.	Clover cwt.	Approximate ratio: total to clover
First cut (April)	7.50	0.28	27 : 1
Second cut (May)	10.40	1.21	9 : 1
Third cut (July)	17.42	4.02	4 : 1
Fourth cut (Sept.-Oct.)	12.305	3.21	4 : 1

At the beginning of the grazing season clover contributed a trifling amount to the available herbage; in May it is higher but still only about one-ninth. During the rest of the year it averaged about one-fourth of the total. It is, therefore, during the months when grazing is likely to be short that clover makes its greatest contribution.

SUMMARY

Experiments over six years on the use of different kinds and amounts of nitrogenous fertilizers on small plots of permanent pasture are described and summarized.

Up to a level of 4.5 cwt. sulphate of ammonia per acre applied in February there was a proportionate response in dry matter production

in April. Omitting the single year when scorching occurred, the average increase per cwt. of sulphate of ammonia applied was 2.3 cwt. dry matter with an additional 0.85 cwt. in the second (May) cut. The average recovery of the nitrogen applied in February was 35.9% in April, and 8.6% in May.

With nitrogen applied in June the response in dry matter production in July and September–October was similar, but the recovery varied widely with the varying effect of nitrogen on clover production. With heavy depression of clover, percentage recovery was low or negative.

On plots not receiving nitrogen the dry matter production for the whole year was at the rate of 1.92 cwt. per inch of rain reckoned on the harvest year (Oct.–Sept.). The largest variation from this was only 0.1 cwt.

For the whole year the response to nitrogen was greatest in the years of lowest rainfall.

The nitrogen applied in February considerably increased the protein in the “grasses” at the first cut, and to a small extent in the second cut. For the third and fourth cut it is suggested that the protein differences are correlated with differences in amounts of clover.

For the first cut of the year “clovers” also show a much higher protein content on the nitrogen plots.

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FIELD EXPERIMENTS ON THE EFFECT OF APPLYING A NITROGENOUS FERTILIZER TO WHEAT AT DIFFERENT STAGES OF GROWTH

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IN pot-culture experiments previously reported (Watson, 1936), it was found that a nitrogenous fertilizer applied at any time up to the end of May increased the yield of wheat grain to approximately the same extent, but a very late application after ear emergence produced no detectable increase of yield. The increase in the yield of straw was greatest when the nitrogenous fertilizer was applied immediately after germination, steadily decreasing with later applications. Early application tended to increase the yield of grain by increasing the number of ears per plant. Later applications had a smaller effect on ear number, but increased the number of grains per ear and the 1000-corn weight. The variations in straw yield with time of application of the nitrogenous fertilizer were almost entirely accounted for by variations in the number of shoots. No evidence was found of variation in the length of straw with time of application, but as only the length of the main shoot was measured, it is possible that the mean height of all shoots was affected. The nitrogen uptake in the whole plant was independent of the time of application, but with later application nitrogen as percentage of dry matter increased in both grain and straw, and a greater proportion of the total nitrogen content of the plant was found in the grain.

The most obvious difference between field conditions and those of pot culture is in water supply. In the field, excessive rainfall may leach the added nitrogenous fertilizer from the neighbourhood of the roots, while deficient rainfall may cause the surface of the soil to become so dry that the nitrogenous fertilizer cannot be absorbed by the roots, or may directly limit the growth of the plant. In pot culture, water shortage and drainage from the soil can both be avoided; thus the results obtained measure the ability of the plant to take up and utilize in growth a given quantity of nitrogenous fertilizer presented to it at different stages of growth. In field experiments the effect of meteorological factors, in

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altering the availability to the plant of the nitrogen supplied, is superimposed on the direct effect on the plant.

The Broadbalk experiment at Rothamsted, where wheat is grown continuously on the same plots with the same manuring in successive years, provides a comparison of the effects of autumn and spring applications of nitrogenous fertilizers. In the early years of this experiment the whole of the nitrogenous fertilizer was applied in the autumn, but from 1884 onwards most of it has been applied in the spring and only a small part in the autumn, except on one plot which has continued to receive an autumn dressing. This plot has given a lower average yield of both grain and straw than the corresponding plot which receives a spring application (Table I).

Table I. *Mean yield of plots 7 and 15, Broadbalk field, 1884-1925*

Plot	Treatment	Yield, cwt. per acre	
		Grain	Straw
7	$\frac{1}{2}$ N in autumn, $\frac{3}{2}$ N in spring	16.8	30.4
15	All N in autumn	14.9	26.3

Both plots received 412 lb. sulphate of ammonia per acre, and in addition superphosphate and sulphates of potassium, sodium and magnesium.

It might be assumed that the autumn dressing was less effective than the spring dressing because of loss of nitrates from the soil by leaching during the winter months, but contrary to this, "Alumnus" (1932) has shown that the superiority of plot 7 over plot 15 in grain yield is not greatly affected by winter rainfall, but is increased by rainfall above the average in spring and early summer. Plot 15 is more adversely affected by spring rainfall than plot 7, and in years of low spring rainfall the autumn dressing may produce a greater increase of grain yield than the spring dressing. The reason for this is not clear. "Alumnus" suggests that the autumn-dressed wheat has a better chance of establishing a good root system, enabling it to withstand dry conditions in spring more easily than the spring dressed wheat. It is possible that although leaching by winter rainfall occurs, the nitrogen is not removed out of the range of the wheat roots, except when leaching is continued by heavy rain in the spring.

Garner & Sanders (1936) carried out seven field experiments, in three of which application of sulphate of ammonia at sowing was compared with an early spring (February) top-dressing, and with application half at sowing and half as a top-dressing, while in the remaining four a late spring (May) top-dressing, and dressings divided between two of the three

times of application were also included. In three experiments the yield of grain was depressed by all the nitrogen applications—a result which is attributed to the high state of fertility of the soil, and to losses due to lodging and a greater incidence of “foot-rot”. In one experiment none of the nitrogen applications had any significant effect on grain yield. Of the three experiments in which an increased yield of grain was produced by sulphate of ammonia, one showed no difference between times of application, in one the early dressings (at sowing or in February) were superior to the late, and in the third the late were superior to the early. From a comparison of the rainfall and yields during three years Garner & Sanders conclude that, when the winter is wet, autumn dressings are ineffective, whilst May dressings are very beneficial provided that the June rainfall suffices to wash them in; when the winter is dry, early dressings are more effective than late.

Lewis *et al.* (1938) have reported the results of an extensive series of field experiments, carried out at a number of centres over a period of 7 years. In the first group of experiments, times of top-dressing ranging from the end of February to early June were tested. There was no consistent relation of grain yield to time of application. In individual years the results showed a similar variation to those of Garner & Sanders, except that in none of the experiments did the nitrogenous fertilizer depress the grain yield. The increase in the yield of straw produced by the nitrogenous fertilizer consistently showed a decline with later application.

In a second larger group of experiments a comparison was made between early (end of February to early April) and late (end of April or May) top-dressings. In no experiment was a significant difference in grain yield between the times of application recorded, and on the average of all experiments the difference was very small. The average response in straw yield to the early dressing was significantly greater than that to the late, and though in individual experiments this result was reversed, in no experiment was the late dressing significantly superior to the early.

A third series of experiments, restricted to one season, compared an autumn application of nitrogenous fertilizer with an early spring top-dressing, and with a dressing divided between the two times. In three of the experiments the autumn application had no detectable effect on either grain or straw yield, while the spring application gave considerable increases. In the other two experiments autumn application gave a greater increase of grain and straw yield than late application. At the two centres where the autumn dressings were superior to the spring, the winter rainfall, particularly in December, was very much lower than at

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the centres where the autumn dressings failed. The divided dressings consistently gave results intermediate between the early and late dressings.

Garner & Sanders found that plant number was unaffected by the nitrogenous fertilizer. There was some evidence that early applications produced a greater shoot and ear number, but a smaller ear size than late, though this did not occur in all experiments. Lewis *et al.* made ear counts in two experiments and found no significant differences between times of application; even late application in May increased the number of ears. The height of the straw was increased by the nitrogenous fertilizer to a greater extent when applied early than when applied later. The 1000-corn weight was not significantly affected.

In the present paper the results of a series of field experiments carried out at Rothamsted and Woburn in the years 1926 to 1936 are presented. Full details of these experiments are given in the Rothamsted Annual Reports for the appropriate years.

RESULTS

First Series, Rothamsted, 1926-31

Yield of grain and straw (Table II).

In this series of experiments early and late spring top-dressings were compared. In every experiment comparisons were made of sulphate of ammonia and muriate of ammonia, applied at the rates of 0.2 cwt. N per

Table II. *Rothamsted experiments, 1926-31. Effect of 0.2 cwt. N per acre applied early or late (mean of sulphate and muriate of ammonia)*

Harvest year	mean yield cwt. per acre		Mean increase, cwt per acre						Date of application	
			Grain			Straw				
	Grain	Straw	Early	Late	S.E.	Early	Late	S.E.	Early	Late
1926	16.3	44.3	1.6 3.7*	3.5 2.0*	±0.99	3.8 7.0*	3.6 3.6*	±2.01	24 March	5 June
1927	25.2	49.2	1.4 3.4*	1.3 2.8*	±1.26	4.1 9.7*	3.5 3.2*	±1.82	11 April	30 May
1928	25.1	33.2	0.6	2.1	±0.74	2.1	4.4	±1.22	14 March	25 April
1929	17.6	26.7	1.8	1.8	±1.62	4.9	3.9	±1.65	18 March	13 May
1930	15.1	24.4	-0.1	0.3	±0.59	2.8	2.1	±0.32	31 March	15 May
	26.7	60.1	-2.1	0.0	±1.51	5.4	2.5	±2.91	27 March	16 May
1931	21.2	44.3	1.2	0.2	±0.31	6.8	5.1	±0.75	20 March	1 May
Unweighted mean	(a)		0.92	1.31	±0.383	4.90	3.56	±0.589		
	(b)		0.63	1.31	±0.416	4.27	3.59	±0.650		
Weighted mean	(a)		1.12	0.81	±0.228	3.63	2.76	±0.269		
	(b)		0.89	0.67	±0.239	3.43	2.75	±0.275		

* Double rate, 0.4 cwt. N per acre.

(a) Including mean of single and double rates for 1926 and 1927.

(b) Excluding double rate.

acre, and in 1926 and 1927 also at double this rate. In 1928 and 1929 the fertilizer treatments were applied to several varieties, but no significant interactions of variety with fertilizer were found.

The increases in grain yield produced by the top-dressings were small, and rarely significant, except when applied at the double rate. In only one experiment (1931) was the difference between times of application significant, and here the early dressing increased the grain yield while the late dressing had no effect. On the average of all the experiments, both early and late dressings significantly increased the grain yield, but the difference between the times of application was not significant.

The early dressing consistently gave a greater increase of straw yield than the late dressing, the only exception being 1928, but the difference between times of application was significant on only one occasion (1927, double rate). On the average of all experiments, when the results of individual experiments are weighted inversely as the error variance, so that the more accurate experiments receive greater weight, the superiority of the early over the late dressing was significant.

Growth observations (Table III).

A number of counts and measurements of various growth attributes were made during the course of these experiments, and these are summarized in Table III.

Table III. *Rothamsted experiments, 1928-31. Effect of 0.2 cut. N per acre, applied early or late (mean of sulphate and muriate of ammonia)*

	Ear number per metre				Ear length, cm				Shoot height, cm			
	Increase				Increase				Increase			
	Mean	Early	Late	S.E.	Mean	Early	Late	S.E.	Mean	Early	Late	S.E.
1928	43.5	2.07	5.52	± 2.02	8.5	0.48	0.67	± 0.266	83.0	5.58	0.78	± 1.56
1929	20.1	0.38	0.44	—	—	—	—	—	—	—	—	—
1930	58.5	2.32	1.07	± 2.03	4.6	0.24	0.35	± 0.080	—	—	—	—
1931	36.4	-0.18	4.52	± 2.36	—	—	—	—	78.8	4.66	0.10	± 3.22
Mean*	—	1.59	3.70	± 1.36	—	0.36	0.51	± 0.139	—	5.12	0.44	± 1.79

* Excluding 1929.

The late top-dressing gave a greater number of ears per metre than the early in three out of four experiments, but on the mean of all the counts the difference between times was not significant.

There is some evidence that the late dressings produced larger ears and shorter straw than the early dressings.

Second Series, Rothamsted and Woburn, 1934-6

In this series an attempt was made to obtain results of wider application, by carrying out similar experiments each year on the heavy clay soil of Rothamsted, and the sandy loam of Woburn.

Latin square arrangements were used for all the experiments. The treatments were a series of times of application of a dressing of sulphate of ammonia (0.3 cwt. N per acre in 1934 and 0.4 cwt. N per acre in the other years) ranging from the time of sowing to early June. Every experiment also included a no-nitrogen treatment. In 1933-4 at Rothamsted there were seven times of application and at Woburn six. In the other four experiments there were five times. Table IV gives the previous cropping and manuring of the experimental sites, and the dates of sowing and of harvest. In this and subsequent tables, the experiments are denoted by the harvest year, though some of the relevant dates, e.g. that of sowing, belong to the previous year.

Table IV. *Agricultural details of experiments*

Exp.	Previous crop	Manuring of previous crop per acre	Date of sowing	Date of harvest
Rothamsted				
1934	Beans	2 cwt. superphosphate, 2 cwt. 30 % potash salts	12 October	6 August
1935	Beans	None	26 October	9 August
1936	Beans	None	28 October	18 August
Woburn				
1934	Potatoes	25 tons dung, 2½ cwt. sulphate of potash, 2½ cwt. super-phosphate	6 November	1 August
1935	Potatoes	12 tons dung, 3 cwt. super-phosphate, 2 cwt. sulphate of potash	8 November	2 August
1936	Fallow	None	25 October	19 August

The same variety of wheat, Victor, was used throughout. At Rothamsted the drill rows were spaced 6 in. apart, and at Woburn 8 in. Some of the experiments were harvested by the sampling method. All the grain yields recorded are the total yields of undressed grain.

In the 1935 and 1936 experiments the nitrogen applications were made at similar times, viz. 0, 12, 20, 26 and 30 weeks after sowing, except that in the Woburn experiments the first application was made 2-4 weeks after sowing. In the 1934 experiments there were no applications 12 weeks after sowing, but for ease of presentation in the tables, means for the applications 8 and 14 weeks after sowing at Rothamsted, and 10 and 16 weeks after sowing at Woburn, are entered in the column headed

"12 weeks after sowing". The last application at Rothamsted in 1934, 34 weeks after sowing, is omitted from the tables. This method of presentation makes no appreciable difference to the results.

Table V. *Yields of grain and straw*

	No nitrogen	Time of application of nitrogen, weeks after sowing					S.E.	Mean of all applications	S.E.
		0	12	20	26	30			
		October* December†	January	March	End April	End May			
Grain, cwt. per acre									
Rothamsted									
1934	35.0	37.1	38.0	36.4	37.0	35.0	1.39	36.7	0.57
1935	30.7	31.1	28.6	29.5	31.1	32.5	0.96	30.6	0.43
1936	30.6	31.9	29.3	29.4	29.5	30.8	0.50	30.2	0.22
Mean	32.1	33.4	32.0	31.8	32.5	32.8	0.59	32.5	0.26
Woburn									
1934	12.1	11.8	11.2	11.4	12.8	12.3	0.78	11.8	0.32
1935	25.3	30.2	32.4	27.0	32.7	32.7	0.65	31.0	0.29
1936	13.4	17.7	19.3	20.5	21.6	18.9	0.56	19.6	0.25
Mean	16.9	19.9	21.0	19.6	22.4	21.3	0.39	20.8	0.17
Straw, cwt. per acre									
Rothamsted									
1934	52.3	56.9	56.0	56.5	55.9	50.9	2.50	55.2	1.02
1935	57.7	64.8	68.2	66.9	65.1	64.8	1.07	66.0	0.48
1936	10.8	45.2	51.3	50.8	45.3	45.6	0.80	47.6	0.35
Mean	50.3	55.6	58.5	58.1	55.4	53.8	0.94	56.3	0.42
Woburn									
1934	32.8	33.1	31.2	31.0	29.0	27.6	2.18	30.5	0.89
1935	31.1	45.6	48.7	48.1	44.8	37.6	1.34	45.0	0.60
1936	22.4	31.3	38.4	40.8	36.1	34.9	1.04	36.3	0.46
Mean	28.8	36.7	39.4	40.0	36.6	33.4	0.92	37.2	0.41

* Rothamsted † Woburn.

Yield of grain (Table V).

The effect of the nitrogenous fertilizer on grain yield at Rothamsted was small, and in no year was the mean increase for all times of application significant. In 1935 and 1936 the results indicate a slight depression. This, however, was restricted to the intermediate times of application; application at sowing or at the end of May apparently gave an increase. In 1936, the application at the time of sowing gave a significantly greater yield than those made in January, March and April.

There was no trace of any effect of the nitrogenous fertilizer on grain yield at Woburn in 1934, but in 1935 and 1936 large increases were found, despite the fact that the 1935 experiment followed a well-manured potato crop and the 1936 experiment a bare fallow. The yields for the different times of application varied significantly in both 1935 and 1936. In 1935 there was no regular relation of yield to time of application, but in 1936 the yield steadily increased with later application up to 26 weeks after sowing, falling again at the latest application. This is the reverse of the result for Rothamsted in the same year.

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The mean increase of grain yield of all experiments and for all applications of sulphate of ammonia at Rothamsted was only 0.4 cwt. per acre and was not significant. At Woburn the mean increase was 3.9 cwt. per acre. On the average of all experiments the applications made 20 weeks after sowing (March) were somewhat less effective than earlier or later applications, but the differences between times of application are all small, and the mean values serve to emphasize rather the uniformity of the effect of the nitrogenous fertilizer whatever the time of application. There is no suggestion of any well-defined optimum time of application, nor is there any indication that applications at the time of sowing were less effective than spring or summer top-dressings.

Yield of straw (Table V).

The sulphate of ammonia applications had no significant effects on the yield of straw in 1934 at either Rothamsted or Woburn. At Woburn there is some indication of a fall with later application. In the other years large increases of straw yield were obtained, and all the experiments show a similar relation between time of application of sulphate of ammonia and the increase of yield produced. The maximum increase in each year was given by the January or March applications. There was a steady decrease of yield with later application, and the applications at the time of sowing were also less effective. This relationship between straw yield and the time of application of the nitrogenous fertilizer, expressed as a quadratic regression, was significant in all four experiments of 1935 and 1936.

The mean increase of straw yield for all times of application, like that of grain yield, was greater at Woburn than at Rothamsted, but was significant at both centres. The relationship of the yield of straw to time of application is quite regular. The optimum time of application appears to be slightly later at Woburn than at Rothamsted. On the average of all experiments the latest applications at the end of May or in early June gave a smaller increase of straw yield than application at the time of sowing.

Relation between yield of grain and rainfall.

The uniformity of the mean yields of grain shown in Table V suggests that, in general, the effect of the nitrogenous fertilizer on grain yield is independent of the time of application within the range tested in the experiments, and that the variation in the yield of grain between times of applications in individual years is caused by seasonal differences in

climatic factors altering the availability to the plant of the nitrogen supplied. Rainfall is likely to be the most important factor, but the number of experiments is far too small for a full analysis of rainfall effects.

If the action of additional rainfall is qualitatively the same at all times of the year, it might be expected that within each year the increase of yield produced by the nitrogenous fertilizer would be correlated with the amount of rain falling within a fairly short period immediately after the time of application of the fertilizer. This was tested by fitting linear regressions of the increase of yield of grain on rainfall during a period of 4 weeks after the time of application, for each experiment. The period of 4 weeks was chosen arbitrarily, but similar results are obtained if a slightly longer or shorter period is used. The regression coefficients are given in Table VI.

Table VI. *Regression coefficients of increase of yield of grain, in cwt. per acre, on rainfall in inches during 4 weeks after time of application of the nitrogenous fertilizer*

	Rothamsted	Woburn
1934	-0.052 \pm 0.631	-0.935 \pm 0.558
1935	0.742 \pm 0.563	-1.989 \pm 0.586
1936	0.413 \pm 0.103	-1.206 \pm 0.241

The regression coefficients for Woburn were all negative and those for 1935 and 1936 are significant. Thus, the effect of the nitrogenous fertilizer on the yield of grain decreased with increase in the amount of rainfall immediately after the time of application. Such a result would be expected if the effect of heavy rainfall is to leach the added nitrogen from the soil before it can be taken up by the plant.

The results for Rothamsted are very different. There is no trace of any correlation between the effectiveness of the nitrogenous fertilizer and rainfall in 1934, and the regression coefficients for 1935 and 1936 are positive, but that for 1935 is not significant. This evidence, though not conclusive, suggests that the effectiveness of the nitrogenous fertilizer at Rothamsted is increased by additional rainfall in the period immediately after the time of application.

It is obvious that information on the rate of uptake of the added nitrogen by the plant, and on the depth distribution of nitrogen in the soil, is essential for a full explanation of these rainfall effects. Without such information it seems unprofitable to suggest possible mechanisms for the Rothamsted results, nor is it certain that the Woburn results are to be explained in terms of leaching. The most that can be said is that rainfall immediately after the time of application of the nitrogenous

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fertilizer appears to have a marked influence on the effectiveness of the fertilizer, and that the effects of rainfall differ on the heavy soil of Rothamsted and the light soil of Woburn.

Growth observations (Table VII).

Counts of plant and shoot number per metre of drill row, and measurements of shoot and ear height were made at intervals during the growth of the crops. Shoot height before ear emergence was measured from the ground to the auricle of the highest leaf. Ear height, at or close to harvest, was measured from the ground to the tip of the ear. The counts of plant and shoot number were made on two randomly located samples per plot, each consisting of two $\frac{1}{2}$ m. lengths of neighbouring drill rows. Shoot and ear height were determined for eight shoots per plot.

Many of the early observations were made before all the nitrogen treatments were applied. On these occasions, the plots which subsequently received sulphate of ammonia were included in the "no-nitrogen" treatment mean, which consequently has a different standard error from the means for the different times of application of nitrogen.

No significant differences between treatments in plant number were found at any time. In 1934 at Rothamsted a count was made at harvest by digging up and separating the plants. The mean number per metre had decreased from 46 in December to 39 in August, but there was no evidence that any of the nitrogen treatments had caused an increased survival of plants. Plant number was consistently greater at Rothamsted than at Woburn.

The early shoot counts during March showed no significant treatment effects, but a tendency for shoot number to be increased by the nitrogen applications was apparent, except at Woburn in 1934. This effect was intensified in the later counts and persisted in June and July when many shoots had died.

In April and May, at about the time of maximum shoot number, the January application of nitrogen usually produced a greater increase of shoot number than earlier or later applications. At Rothamsted in 1934, however, the application at the time of sowing produced the greatest increase. In the June and July counts there were no significant differences in shoot number between times of application of nitrogen.

Shoot height and ear height were consistently increased by the nitrogenous fertilizer, and the January and March applications usually had the greatest effect. Late applications at the end of May or in early June had little or no effect on shoot and ear height.

Table VII. *Observations made during growth*

	Date	No nitrogen	S.E.	Time of application of nitrogen, weeks after sowing						Mean of all applications	S.E.
				Shoot number per metre of drill-row					End May		
				0 October* December†	12 January	20 March	26 End April	30			
Rothamsted 1934	2 March	53	2.4	67	58	62	—	—	—	61	2.4
	26 April	111	5.2	134	126	127	103	—	—	123	4.1
	21 June	57	4.6	65	60	64	64	—	64	63	1.9
	20 March	161	7.2	186	167	169	—	—	—	174	7.2
	12 July	72	4.0	72	74	80	67	81	—	75	1.8
1936	25 March	84	3.2	91	90	84	—	—	—	88	3.2
	5 May	96	3.5	89	128	115	95	—	—	107	2.5
Woburn 1934	23 March	49	2.0	50	46	—	—	—	—	48	2.3
	4 May	125	4.4	133	154	136	—	—	—	149	3.8
	15 June	58	3.6	55	60	61	50	60	—	58	1.5
	8 April	124	5.2	144	179	120	—	—	—	148	5.2
	3 April	72	3.9	73	96	75	—	—	—	81	3.9
1936	6 May	61	3.4	68	120	104	64	—	—	89	2.4
	26 July	43	3.2	52	52	57	51	53	—	53	1.4
Shoot height, cm.											
Rothamsted 1936	5 May	4.3	0.28	4.2	6.1	5.8	4.0	—	—	5.0	0.20
Woburn 1934	4 May	9.5	0.34	11.2	12.2	10.5	—	—	—	11.5	0.29
	25 May	23.6	1.34	25.9	27.4	25.4	24.3	—	—	26.1	0.85
	8 April	2.6	0.13	2.7	3.7	2.6	—	—	—	3.0	0.13
	6 May	3.5	0.28	4.1	5.9	6.3	4.5	—	—	5.2	0.20
	26 July	57.5	2.61	65.1	82.0	86.0	73.7	60.4	—	73.4	1.17
Ear height, cm.											
Rothamsted 1935	12 July	116	2.6	119	125	125	126	113	—	122	1.2
1936	11 August	103	2.2	112	121	117	111	107	—	114	1.0
Woburn 1935	25 July	105	2.5	121	118	121	114	117	—	118	1.1
	26 July	80	3.7	90	111	112	103	88	—	100	1.7

* Rothamsted. † Woburn.

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Analysis of yield of grain (Table VIII).

At harvest, an analysis of the yield of grain was made in terms of ear number, number of grains per ear and 1000-corn weight. Counts were made of the number of ears per metre of drill row in two random samples per plot and of the number of grains in eight ears per plot. A determination of 1000-corn dry weight was made for each plot.

Table VIII. *Observations at harvest. Analysis of yield of grain, and nitrogen content of grain and straw*

		Time of application of nitrogen, weeks after sowing								
	No nitrogen	0 October* December†	12 January	20 March	26 End April	30 End May	s.e.	Mean of all applications	s.e.	
Ear number per metre of drill row										
Rothamsted										
1934	50.6	61.5	60.6	62.5	50.2	56.5	3.68	60.1	1.50	
1935	69.6	70.4	72.3	78.3	65.3	78.9	3.88	73.0	1.73	
1936	55.0	49.2	58.0	48.5	49.4	51.6	3.32	51.3	1.48	
Woburn										
1935	46.8	57.3	62.2	55.2	55.3	48.0	3.73	55.6	1.67	
1936	38.0	46.7	47.8	53.7	46.8	47.2	2.77	48.4	1.24	
Number of grains per ear										
Rothamsted										
1934	46.2	46.4	48.8	49.2	48.4	48.6	1.35	48.3	0.55	
1936	32.0	44.1	37.9	32.0	36.4	39.9	1.83	38.1	0.82	
Woburn										
1936	30.8	38.3	37.4	42.0	43.8	44.6	2.06	41.2	0.92	
1000-corn dry weight										
Rothamsted										
1934	30.4	28.9	29.8	28.8	29.3	28.7	0.44	29.1	0.18	
1935	34.2	32.8	31.5	32.9	32.8	31.6	0.51	32.3	0.23	
1936	34.0	32.4	31.8	31.8	30.3	29.1	0.32	31.1	0.14	
Woburn										
1935	39.7	37.6	37.9	37.5	35.4	38.6	0.51	37.4	0.23	
1936	34.9	35.6	33.9	33.7	33.2	29.3	0.40	33.1	0.18	
Grain, nitrogen as percentage of dry matter										
Rothamsted										
1934	2.13	2.26	2.22	2.18	2.22	2.27	0.047	2.23	0.019	
1935	1.85	1.96	2.02	1.91	1.94	1.98	0.026	1.96	0.011	
1936	1.90	1.96	1.98	1.98	2.07	2.12	0.022	2.02	0.010	
Woburn										
1934	2.98	3.02	3.20	3.14	3.21	3.20	0.104	3.13	0.042	
1935	1.80	1.76	1.79	1.76	1.80	1.98	0.035	1.82	0.016	
1936	1.73	1.72	1.60	1.68	1.67	1.75	0.046	1.68	0.021	
Straw, nitrogen as percentage of dry matter										
Rothamsted										
1934	0.35	0.45	0.41	0.40	0.42	0.42	0.019	0.42	0.008	
1935	0.36	0.43	0.51	0.42	0.49	0.47	0.020	0.46	0.009	
1936	0.44	0.42	0.46	0.42	0.50	0.54	0.013	0.47	0.006	

* Rothamsted. † Woburn.

(a) *Ear number per metre of drill row.* The ear number at harvest was not significantly affected by the nitrogenous fertilizer in any of the Rothamsted experiments, but in the two Woburn experiments for which data are available, the ear number was considerably increased. In the 1935 Woburn experiment the increase in ear number declined with later

application of nitrogen, and that produced by the application 30 weeks after sowing was only very small. In the 1936 Woburn experiment, there were no appreciable differences between times of application, and the latest application was equally as effective in increasing the number of ears as the earlier applications.

(b) *Number of grains per ear.* The nitrogenous fertilizer increased the number of grains per ear in all three experiments for which data are available, but not significantly in the 1934 Rothamsted experiment. At Woburn in 1936, the increase was greater the later the time of application, but at Rothamsted in the same year, the earliest and latest times of application gave higher numbers of grains than the intermediate times, and application in March produced no increase.

(c) *1000-corn weight.* The 1000-corn weights are all low, partly because they were made on undressed samples of grain.

The 1000-corn weight was depressed by the nitrogenous fertilizer, on the mean of all times of application, in all the experiments. There were no significant differences between times of application at Rothamsted in 1934 or 1935. In 1935 at Woburn, application 26 weeks after sowing produced a greater depression than at other times. In both of the 1936 experiments the depression of 1000-corn weight steadily increased with later application.

These results agree with the results of Papadakis & Talellis (1937), who found in a pot-culture experiment that all applications of nitrogen before ear emergence depressed the 1000-corn weight, though application after ear emergence caused an increase. In the Rothamsted pot experiment (Watson, 1936), late spring applications before ear emergence, as well as applications after ear emergence, increased the 1000-corn weight. No satisfactory explanation of this difference between the field and pot-culture results can be offered.

Nitrogen content as percentage of dry matter (Table VIII).

Determinations of nitrogen content were made on the grain of all experiments, and on the straw of the Rothamsted experiments. For this purpose, samples from the replicate plots were bulked so as to give duplicate samples of each treatment.

(a) *Grain.* In the Rothamsted experiments the nitrogenous fertilizer increased the nitrogen content of the grain, on the average of all times of applications. The results of the Woburn experiments were less regular, and the average response to nitrogen was not significant in any year. In only two experiments, at Woburn in 1935 and at Rothamsted in 1936,

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were there significant differences between times of application. Here the nitrogen content of the grain increased with later application of the nitrogenous fertilizer.

No evidence was found of a consistent relation between the nitrogen content of the grain and yield except in the Woburn experiment of 1935, for which the regression coefficient of nitrogen percentage of the grain on yield of grain for the different times of application was found to be significantly positive. In this experiment, therefore, high nitrogen content was associated with high yield.

(b) *Straw.* Application of the nitrogenous fertilizer increased the nitrogen content of the straw in all three years at Rothamsted, but in 1936 the increase was restricted to the late applications in April and May, and the early applications had no effect. There were no significant differences between times of application in 1934 and 1935.

Lodging.

Lodging occurred in the experiments at Rothamsted in 1927, 1929, 1930, 1931, 1935 and 1936, but there was none in the Woburn experiments. In 1929, lodging affected all the plots at one end of the experiment and was not related to fertilizer treatment. In 1930, the whole experiment was badly laid, though the plots which received no nitrogen appeared to have suffered slightly less than the others. A similar result was found in the 1936 experiment; the plots which received top-dressings, whatever the time of application, were almost completely lodged, but the lodging was less severe where the nitrogen was applied at sowing, and still less where no nitrogen was given.

The other three experiments showed clearer differences between times of application. Of the forty-eight plots of the 1927 experiment, seven were recorded as lodged. Four of these received the early dressing of nitrogen at the double rate; three were badly lodged and one slightly. Slight lodging occurred on one plot of each of the remaining nitrogen treatments—early and late dressings at the single rate, and the late dressing at the double rate, but none of the unmanured plots was lodged.

In 1931 all the plots were wholly or partially lodged, and the worst affected had to be cut by scythe. The plots treated in this way were distributed between treatments as follows: no nitrogen 3; early top-dressing 6; late top-dressing 3; double dressing, half applied early and half late, 9.

Lodging was patchy in the 1935 experiment, and an eye estimate was

made of the fraction of the area of each plot which was laid. The treatment means were:

	Time of application of nitrogen					
	Weeks after sowing					
Area laid, as fraction of total	Nitrogen	0	12	20	26	30
	0	0.05	0.6	0.55	0.3	0.2

All the unmanured plots were standing, and only a very small part of the plots which received nitrogen at the time of sowing was laid. About two-thirds of the area which received a January application was lodged, and the fraction steadily decreased with later application to one-fifth for the late May application.

These results show that early spring top-dressings increase the susceptibility to lodging to a greater extent than late top-dressings. This is in accordance with the observed variation of straw yield and shoot height with time of application. The difference between early and late top-dressings was not very clear cut, and it never happened that the plots which received a late top-dressing were completely free from lodging, when the early dressed plots were wholly or partially laid. The tendency to lodge was not much affected by applications of nitrogen at the time of sowing.

DISCUSSION

The results of the experiments of Garner & Sanders, and Lewis *et al.*, and those presented in this paper, agree with the pot-culture results in that, on the average of a number of years, they give no indication of any consistent variation in the increase of yield of grain produced by a nitrogenous fertilizer with time of application ranging from sowing to the end of May. In individual years, however, the effectiveness of the nitrogenous fertilizer varied with the time of application. It seems justifiable to conclude that the ability of the plant to utilize the additional supply of nitrogen in increasing the yield of grain is independent of the time of application of the nitrogenous fertilizer, and that the variation between times of application found in individual years is determined by the particular weather conditions of the season. The Broadbalk results differ from the others in showing that an autumn dressing is less effective than a spring dressing. It is possible that this is related to some character of the general trend of seasonal weather conditions at Rothamsted, and if experiments were conducted over a long period of years, similar differences between times of application, say, for example, between early and late spring top-dressings, might be found associated with the seasonal

climatic trends of particular districts. It must be noted, however, that the wheat on Broadbalk is grown in conditions which differ widely from those of normal agricultural practice. Apart from these considerations, the available data indicate that it is not possible, on the basis of grain yield alone, to select any one particular time of application as the most advantageous.

Though it is probable that the amount and distribution of rainfall are the most important of the factors which determine the differences between times of application in the effectiveness of the nitrogenous fertilizer in individual years, there is little information available about the nature of rainfall effects. Garner & Sanders and Lewis *et al.* present evidence to show that high winter rainfall reduces the effectiveness of autumn applications of nitrogen. This is confirmed by the Broadbalk results, but "Alumnus" has shown that winter rainfall has almost as great an adverse effect on the grain yield of plots receiving a spring top-dressing, as on that of the plot which receives all its nitrogen in the autumn, and the relative effectiveness of spring and autumn dressings is dependent more on spring and early summer rainfall, than on winter rainfall. It has been shown that at Woburn rain falling immediately after the time of application appears to depress the effectiveness of the nitrogenous fertilizer in increasing the yield of grain; at Rothamsted the effects are less definite, but are in the opposite direction.

The relation of the yield of straw to time of application varied less from year to year than that of grain yield. Early spring top-dressings gave a greater increase of straw yield than late spring or early summer top-dressings, and, usually, than applications at the time of sowing. The optimum time of application for straw yield lies in the period from January to March. These results partially confirm those of the pot experiment, the main difference being that in pot culture, autumn application was found to give the greatest increase of straw yield, the increase declining steadily with later application. The small effect of autumn dressings on straw yield in field conditions may be due to adverse effects of the normal winter rainfall. In the pot experiment it was found that differences in straw yield could be accounted for almost entirely by differences in shoot number at harvest. This is not true of the field experiments, in which the shoot number at harvest varied little with time of application. As the shoot height at harvest showed a variation with time of application similar to that of straw yield, it appears that the treatment effects on straw yield were determined by differences in the weight of straw per shoot, rather than by differences in shoot number.

The results of the field experiments do not substantiate the general statement, which is frequently made, and which is borne out by the pot-culture results, that early nitrogen applications increase the yield of grain by increasing the number of ears, while late applications have a smaller effect on ear number but also increase ear size. It appears that the nature of the effect on the plant depends so much on seasonal climatic conditions, that the relationship to time of application which is found in the more favourable conditions of pot culture, is obscured in field conditions. The determinant of the type of response in the plant must be the time at which the nitrogen applied is taken up by the plant in relation to its stage of development, and not the time of application of the fertilizer to the soil. In the field it is possible that particular weather conditions, such as deficient rainfall or excess rainfall leading to leaching of the nitrogen to a lower depth of the soil, may cause the uptake of nitrogen by the plant to be delayed for a long period after the time of application. An effect of this nature may possibly explain results such as that of the application at sowing in 1936 at Rothamsted, where an early dressing produced effects which, in the pot experiment, were typical of a late dressing.

The common practice in this country is to apply the nitrogenous fertilizer as a top-dressing in February or March. The choice of this time is probably determined mainly by convenience. As soon as the soil becomes sufficiently dry in spring it is usual to harrow and roll wheat, and it is convenient for the top-dressing and cultivations to be carried out together. Applications made at about this time had an effect on the crop in April and May which was more obvious to the eye than that of earlier or later applications. The plants could readily be distinguished by their greater shoot number and height (see Table VII) and by their darker green colour. This obvious and often spectacular effect of early spring top-dressing may possibly account in part for their popularity.

As the increase in the yield of grain, on the average of a period of years, is almost the same whatever the time of application, the most favourable time of application in agricultural practice must be determined from considerations other than the effect on grain yield. Early spring top-dressings produce the greatest increase of straw yield, and are therefore to be recommended if a heavy straw crop is desired. In mechanized corn growing conditions, where straw is a nuisance rather than an asset, it would be advisable to delay the application of nitrogen until May, so as to secure as large an increase of grain yield as with an early top-dressing, but a smaller increase of straw. The May application

also has the advantage that it does not increase the susceptibility to lodging so much as an early top-dressing. The average difference in straw yield between March and May applications has been 1-2 cwt. per acre, where the rate of application was 0.2 cwt. N per acre, and about 5 cwt. per acre in the Rothamsted and Woburn experiments in 1933-6, where the higher rate of application, 0.4 cwt. N per acre, was used. It is doubtful whether the slight advantage of May applications, in reducing the tendency to lodge, offsets this sacrifice of straw yield sufficiently to justify a recommendation that May applications should be used in all circumstances in preference to early spring applications.

Applications of nitrogen at the time of sowing appear to have no special advantage. It has sometimes been suggested that they may assist in the establishment of the plant, and enable it to withstand adverse weather conditions during the winter. Counts of plant number made by Garner & Sanders and in the present experiments do not support this view. The Broadbalk results show that autumn applications may be less effective in increasing grain yield than spring top-dressings, but the other experiments do not indicate that this is true of normal agricultural conditions.

Garner & Sanders have advocated the division of the nitrogenous fertilizer into two dressings, one applied at sowing and the other in May, on the grounds that one of the applications will be effective, the weather determining which. It is unlikely that this system would give a greater increase of grain yield, over a period of years, than if the whole dressing were applied in spring. The variation in the effect on grain yield from year to year might be less than with a single dressing, but against this advantage of stability must be set the additional labour cost of a double application.

The influence of time of application on the quality of the grain as measured by its nitrogen content and 1000-corn weight was too small and irregular to be of much importance in determining agricultural practice. The top-dressings in May sometimes gave a greater increase of nitrogen percentage of the grain than earlier applications, as in the pot-culture experiment, but in one season they also caused a greater depression of 1000-corn weight. In the pot experiment, an application of nitrogen at the end of June after ear emergence, considerably increased both nitrogen percentage and 1000-corn weight, but did not increase the yield of grain. Such late applications would be impracticable in the field, for they could not be applied with a manure drill, without greatly damaging the crop.

SUMMARY

An account is given of the results of two series of field experiments carried out at Rothamsted and Woburn in the years 1926 to 1936 on the effect of nitrogenous fertilizers on wheat. In the first series a comparison was made of the effects of early (March) and late (May) top-dressings, and in the second series a range of times of application from sowing to the end of May were tested.

At Rothamsted, the increases of yield of grain produced by the nitrogenous fertilizer were small and rarely significant, but they were greater at Woburn. On the average of all experiments, the effect of the fertilizer on yield of grain was independent of the time of application. In individual years, variation in effectiveness between times of application was found, and this was correlated with the amount of rain falling in a short period after the time of application. At Woburn, the effectiveness of the fertilizer decreased with increase in the amount of rain falling immediately after the application of the fertilizer, but at Rothamsted the effects were less clear and appeared to be in the opposite direction.

The effects on straw yield were relatively greater, and more consistent, than those on grain yield. A greater increase of straw yield was produced by early top-dressing (January-March) than by application at the time of sowing, and the increase declined steadily the later the time of top-dressing. Shoot height was increased by the nitrogenous fertilizer, and varied with time of application in a similar manner to straw yield.

An analysis of the yield of grain in terms of ear number, number of grains per ear and 1000-corn weight gave results which varied greatly from year to year. The widely held view that early applications of nitrogen increase the yield of grain by increasing the number of ears, while late applications mainly affect ear size, was not confirmed in the field experiments, though it has previously been found to be true for pot cultures.

The effect of the nitrogenous fertilizer on the quality of the grain as measured by its nitrogen content and 1000-corn weight also varied with the season. The 1000-corn weight was usually depressed by the nitrogenous fertilizer whatever the time of application.

The nitrogenous fertilizer increased the susceptibility of the crop to lodging, and early top-dressings had a greater effect than late top-dressings.

The usual practice of applying the nitrogenous fertilizer as a top-dressing in February or March is justifiable on the grounds of convenience, and because applications of nitrogen at this time give as great an increase

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in the yield of grain as later spring top-dressings, and a greater increase of straw yield. But in circumstances where a high yield of straw is not particularly desirable, it would be advantageous to delay the top-dressing until May, and so to minimize the risk of lodging. Applications at the time of sowing appear to have no special advantage.

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INVESTIGATIONS ON CERTAIN TOXIC SUBSTANCES OBTAINED FROM THE WHEAT PLANT WHICH IN- HIBIT THE GERMINATION OF THE UREDOSPORES OF VARIOUS WHEAT RUSTS

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(With Six Graphs)

I. INTRODUCTION

THE study of the physiology of the Uredineae is rendered difficult by the apparent impossibility of growing these fungi in artificial culture; in order to ascertain, therefore, what factors may influence the progress of a particular rust infection, we are forced to investigate the very complex conditions existing within the host plant, in so far as they affect the rust.

In certain problems, however, we may be justified in assuming that the reaction of the rust fungus in the earliest stages of growth, namely in the form of a germ tube from a spore, will be to some extent typical for its later stages, which are never attained in the absence of a living host. One such case is that of reaction to toxins. Whereas it is hard to provide experimental proof that a given substance, toxic to the germinating spore, is also toxic to the actively growing parasite within the host, that is a reasonable assumption, and one substantiated by several cases in the literature, where investigators have found a correlation between the toxicity of substances obtained from the host plant towards the germinating spores of a parasite, and the effective resistance of the host to normal attack (Walker & Lindegren, 1924; Tims, 1926; Sharvelle, 1936).

The present investigation aims at elucidating to some extent the physiology of parasitism among the rusts through a study of certain toxic substances which are produced by the wheat plant, and which inhibit the normal germination of the uredospores of the fungi *Puccinia glumarum tritici* and *P. triticina*.

II. CRITICAL REVIEW OF THE RELEVANT LITERATURE

A number of workers have attempted to obtain information on the mode of parasitism of various fungi by a study of their reactions to solutions obtained from the appropriate and inappropriate host plants. In most cases, they have confined their attention to the effect of these solutions on the germination of the spores of the parasite.

The earliest experiments were those of Ward (1902), who found that the uredospores of *P. dispersa* (= *P. bromina* Erikss.) would germinate equally well in extracts of the host leaves, whether of resistant or susceptible varieties, as in distilled water.

In 1916 Leach (1919) attempted to correlate the susceptibility and resistance of three varieties of wheat to the "species" *P. graminis tritici* and *P. g. tritici-compacti* (now known as a race of the first), with the effect of cold water extracts of their leaves on their spores. He made only a single experiment, for which he gives no figures, but stated that this confirmed the result of Ward given above as to the lack of effect.

More recent work is that of Ezekiel (1930), who made a very painstaking investigation of the effects of extracts of wheat leaves, prepared both with and without heating, on the length of germ tubes produced by the uredospores of various rusts, especially *P. g. tritici*. He claimed that percentage germination (which alone had been measured by previous investigators) was a more variable quantity than the length of germ tubes. Notwithstanding which, it is evident from his figures that the variability of the latter was very considerable in his experiments: so much so, that the conclusions which he draws are hardly justified.

He claims to have established a correlation between the susceptibility of a host variety, and the effect of its extract upon the rust spores. His extracts were obtained by simple pressure, and were found to require considerable dilution before germination could be obtained. Extracts which were prepared with heating were more toxic than those which were uncooked.

Johnstone (1931) carried out experiments on the germination of conidia of *Venturia inaequalis* in various extracts of apple leaves, and found a clear correlation between their toxicity, and the resistance of the respective varieties to infection. She stresses the fact, which seems to have been elsewhere ignored, that the expressed juice may vary rapidly in chemical composition owing to the activity of enzymes. In order to preserve thermolabile components, she did not heat her extracts, but by using them immediately after preparation minimized the effect. There

was no correlation, however, in the case of juices from the fruit. The extracts lost their activity on keeping when in contact with the spores, but not in isolation, and on these grounds she stresses the importance of the interrelation of the enzyme systems of parasite and host in this disease. This subject has been well dealt with by Klotz (1927).

Other workers who have shown clear cases of correlation of this kind are Wiltshire (1915), on *V. inaequalis*, Walker & Lindegren (1924) whose work on the toxic properties of the pigment present in the scales of some varieties of onions to *Colletotrichum* is well known, and, less conclusively, Tims (1926) on *Fusarium conglutinans* on cabbage. The only clear case of this kind among the rusts has been given by Sharvelle (1936), who demonstrated that the extract obtained from a certain variety of flax, highly resistant to the rust *Melampsora lini*, was much more toxic to the spores of this fungus than those from other varieties. But his claim to have established a general correlation is not supported by his figures.

That results of this kind are only of sporadic occurrence in the field of plant pathology is clear from the very diverse results obtained, for example, by Nobécourt (1928), who tried the effect of extracts from a number of unsuitable hosts on various fungi incapable of attacking them. Many allowed good germination of the spores. This is also borne out by certain results in the present work.

The principal criticism which can be raised against those who have studied the rusts from this point of view is their failure to appreciate the degree of variability which exists in the material (germinating spores) irrespective of the refinements used in measuring it. None of the workers cited calculated the standard deviation of their results, and they have generally given these to three or four decimal places. From my own experience, I doubt whether more than one place can be considered valid.

In order to obviate these defects, standard deviations have been calculated for every measurement made, provided that an adequate series of figures was available for the purpose, using the methods of Fisher (1930); in discussing these figures in this paper, the term "standard deviation of a single result" is used to indicate the mean standard deviation found from a number of series of measurements of the same kind. By standard deviation of a mean, is meant the standard deviation of a single result, divided by the square root of the number of figures on which it is based.

In regard to the experimental methods used by previous investigators, they differ from mine in two important respects. In the first place, all (except Ezekiel) confined their attention to uncooked extracts, which

they sterilized if at all by ultrafiltration, whereas in this work the solutions have all been prepared by a process involving heating to 100° C. Secondly, they inoculated the hanging drops in which they carried out their tests by dusting the spores on to the surface, whereas here great care has been taken to ensure the thorough wetting of the spores by the solution. This is probably an important factor in securing uniformity of results, and may partly explain why the present results, though based on a less extensive counting of spores than those of Ezekiel (for example), nevertheless show a greater degree of consistency among themselves.

III. TOXIC SUBSTANCES OBTAINED BY TRITURATION OF LEAVES

The present work has shown that by certain methods toxic substances can be obtained from wheat plants which inhibit the germination of uredospores of rusts.

The first such method adopted was as follows: Leaves from the wheat plants to be tested were ground up with water, and a little fine sand to act as an abrasive, in a mortar; the pulp thus obtained was boiled for a few moments to precipitate some of the proteins, etc., and then centrifuged at about 1000 r.p.m. for a few minutes. On decanting, a clear green solution was obtained. In order that the method might be standardized as well as possible, the amount of water added was made proportional to the weight of the leaves (later, to the dry weight, which was determined separately on a sample of similar leaves), and the length of time elapsing between the grinding of the leaves and the boiling of the pulp was fixed at 10 minutes, so as to keep the activity of enzymes as far as practicable at the same amount.

The solutions thus prepared were toxic to the uredospores of the rusts *Puccinia glumarum tritici* and *P. triticina*, preventing their germination, or reducing it as compared with the controls. The stock culture of *P. glumarum* was derived from a sample found growing naturally on self sown wheat of unknown variety at Long Ashton, and that of *P. triticina* was derived from the stock cultures kept at the Botany School, Cambridge University. The former rust was cultivated on the hosts on which it was found, the latter upon "Wilhelmina" wheat raised from pedigree seed in 5 in. flower-pots. Inoculation was carried out by the usual method, namely the application of uredospores to the upper surface of the first leaf of a seedling (or to any suitable leaf of an older plant) by means of a scalpel sterilized by flaming; the pots were subsequently kept in a humid atmosphere for 2 days by covering them with a bell-jar while standing in a dish of water.

It was thought that the degree of toxicity of the extracts might be correlated with susceptibility to the rusts, and in order to test this a method of assaying the activity of a given solution was evolved. The solution was taken at three concentrations: (a) that resulting from the use of 5 parts by weight of water to 1 part of leaves, when preparing the solution, (b) $\frac{1}{2}$ of the above, and (c) $\frac{1}{4}$ of the above. In each of the three solutions, a suspension of uredospores was prepared, which was made uniform by centrifuging, and then stirring by blowing air through it. From each suspension, two hanging drops were prepared; the size of the drop varied from 12 to 30 μ l., as larger drops tended to spread and run off. The hanging drops were set up in moist chambers (there being two of these on one microscope slide) which were sealed by vaseline at the base only, to ensure adequate aeration. After about 19 hr., the drops were examined under the microscope, and the character of the germination recorded. The percentage germination was estimated to the nearest 10 %, with additional classes of 1 and 5 %, and the length of the germ tubes on an arbitrary scale as "short", "fairly long", "long", or "very long". It is the opinion of the writer that in view of the inherent variability of the material, it is unwise to attempt any more exact measurements, and that attempts (such as those of Johnstone, 1931) to give percentage germination to one or two places of decimals are of little value. The same applies to length of germ tubes.

Results

(a) Comparison of healthy plants of Little Joss wheat with plants infected with *Tilletia caries*.

It is well known that wheat plants normally resistant to *Puccinia glumarum* lose this resistance when infected with bunt, *Tilletia caries* DC. (Tul.) (see Lang, 1917 and Weston, 1927), and the same applies to *Puccinia graminis* (Crépin *et al.* 1938) and *P. triticina*;¹ it was thought that some information on this effect might be obtained from a study of the activity of the toxins obtained by the above method from the healthy and infected hosts. The variety of wheat used in these experiments was Little Joss; in addition a small number of experiments was made on other varieties, with a view to ascertaining in a preliminary way whether the toxicity of the extracts might also be correlated with varietal resistance to rust. (More extensive experiments on this aspect of the question are described below.) All the plants used were raised from

¹ Unpublished results of the author.

pedigree seed grown in the Rockefeller Field, Cambridge. To obtain the bunt-infected plants of Little Joss wheat, seed heavily contaminated with crushed "bunt balls" (parasitized grains) was sown: for field sowing, 25 parts of seed to 1 part bunt-balls were used, and for greenhouse sowing, 10 parts to 1. The activity of the solutions was tested against the uredospores of *P. triticina*. The results obtained are summarized below.

The activity of the solutions is represented in the table as follows: + signifies that germination was obtained first in full-strength solution, ++ that there was germination only in half-strength solution, +++ that it appeared only in quarter-strength solution; the germination at the strengths named being in each case partial only:

Variety	No. of experiments	Activity
Little Joss (healthy)	10	++
Little Joss (bunted)	5	+
American Club (healthy)	2	+++
American Club (bunted)	1	+
Kanred	1	+
Vulgare P.P.	1	++

American Club is a variety of *Triticum compactum*.

It will be observed that the bunted plants of both varieties tested gave a less toxic solution than the healthy plants, thus showing a correlation with their respective resistances; but, in the single comparison made between the other varieties in the healthy state, Vulgare P.P. gave a more toxic solution than Kanred, whereas the latter is much more resistant under field conditions to *Puccinia triticina*.

(b) *Comparison of a selection of different varieties of wheat in respect of the toxicity of the solutions obtained.*

In view of the above result, an experiment was made to determine whether any such correlation could be obtained within a range of English varieties, without reference to infection by any disease such as bunt. Plants of Squareheads, Standard Red, Victor, and Yeoman wheats were grown from pedigree seed supplied by a seed merchant, in 5 in. pots in soil containing a proportion of leaf mould. From the three-leaf stage until about two months old, these plants were used for preparing solutions by the above method from time to time; before each test the pH of the solution was tested by the capillator method, and adjusted, if necessary, to lie between 6.0 and 6.5; in most cases no adjustment was necessary. The uredospores of both species of rust used in this work tolerate pH values between 5.5 and 7.5.

In these experiments, the activity of the solutions was tested on the uredospores of *P. glumarum*, with the following results:

Variety	pH of solution	Percentage germination in solutions of the following concentrations (g./l.)*		
		24.7	12.4	6.2
Squareheads	6.2 (appr.)	0	10	50
	6.2 (appr.)	1	20	50
	6.2 (appr.)	1	5	10
	6.2 (appr.)	0	10	20
Standard Red	6.3	0	10	50
	5.7	1	10	20
	5.7	0	5	—
	6.2	5	30	70
	6.6	10	25	—
Victor	6.1	0	5	10
	6.1	0	30	50
	6.0	0	50	20
	6.2	0	5	30
Yeoman	6.2	0	0	20
	5.7	0	1	20
	6.2	1	10	20
	6.2	0	30	50

* The figures refer to estimated dry matter of original leaf substance and are subject to an error of about $\pm 5\%$.

It will be observed that the above figures do not reveal any consistent differences between the four varieties tested; clearly the difference observed between diseased and healthy plants of Little Joss is of a different order of magnitude from any effect that there may be here, and it is therefore likely that the difference in susceptibility towards rusts induced by the presence of *Tilletia* has a different origin from such differences in susceptibility as exist between the above four varieties. The two rusts, *Puccinia glumarum* and *P. triticina* react very similarly to the solutions used above, as has been demonstrated by a number of tests, and therefore we can hardly attribute the discrepancy to the fact that the two sets of figures were obtained with different rusts.

It will be observed, that the method of preparing the solutions gives us no information as to the presence of the active substances in the living cells of healthy plants, but demonstrates only that these substances appear in the course of the preparation described. To decide this point further experiments were made.

IV. PRESENCE OF TOXIC SUBSTANCES IN LIVING TISSUES

There are two points in the preparation of the solutions where a change in the nature of the substances present is most likely. Firstly, the period between destroying the fresh tissue and boiling the pulp, when autolytic

activity of the enzymes present might be proceeding, and secondly, the heating of the solution. If fresh tissues are air-dried for a period at a temperature of 100° C., their enzymes will be inactivated, and any substances which may be present irrespective of enzyme action will be subjected to the same temperatures as they receive in the method of preparation described before. If, then, solutions prepared from tissues thus dried prove to be inactive, it will be a proof that the active substances are absent in the living cells.

Solutions were therefore prepared in a manner similar to the foregoing, but instead of fresh leaves, leaves which had been dried in an oven at 95° C. were used. This length of drying was found sufficient to bring the leaves to a constant weight. In preparing the extract, water was added to the extent of 40.5 parts by weight by 1 part of dried leaf tissue, so that the full strength solution contained the equivalent of 24.7 g. dry matter per litre. Generally a single leaf was taken, giving a dry weight around 5 mg. from which about 80 μ l. of solution were obtained ultimately, giving two hanging drops with a surplus for pH determinations (where necessary), etc.

Clearly it is with this method unnecessary to standardize the time between trituration and boiling of the solution, since enzyme activity is already prevented.

It was found that solutions prepared by this method were inactive in preventing the germination of the uredospores. The results with the variety Squareheads, using the spores of *P. glumarum* to test the solutions, are given below:

Concentration of solutions g./l.	Number of experiments	Percentage germination	
		Mean %	S.D. %
24.7	8	47.5	13.8
12.4	2	50	—
6.2	2	60	—

Individual tests on other varieties gave similar results.

It should be noted that the spores of *P. glumarum* are very erratic in germination in distilled water, and that with this rust controls have not been introduced in many of the experiments for this reason. Under favourable conditions (in inactive solutions) the percentage germination may reach 90 % but is generally about 50 %, and the attainment of this figure in full strength solutions was taken as a criterion of inactivity. It will be seen that by this standard the above solutions are inactive.

Further experiments were made to detect, if possible, the presence of toxic substances in old and decaying leaves, which, if the hypothesis that the toxins are produced by the autolytic activity of enzymes is correct,

should contain such toxic substances. Relatively few experiments were made, and the results were not altogether conclusive, though it appears that in leaves undergoing a certain type of decay, toxic substances are present. The leaves which gave these active preparations, were withered in appearance, and contained from 30 to 60 % of dry matter. Other leaves were found, however, which were chlorotic and flaccid, at the base of the plants, which had a dry matter content below the average (about 7 %); these leaves did not appear to contain any toxin. The scope of this part of the work is too narrow for any conclusions to be drawn.

One experiment was made, however, in which the triturated pulp was allowed to stand overnight before boiling. In the solution obtained from this, spores would not germinate until it had been diluted to contain about 4 g. per litre of dry matter of the original leaf. This indicates an activity considerably enhanced as compared with the ordinary solutions. (The spores used were of *P. tritici*.) Solutions prepared from decaying leaves, without heating of the material before grinding in the mortar, allowed no germination of *P. glumarum* spores at a dilution of about 6 g. per litre original dry matter.

V. THE PRESENCE OF TOXIC SUBSTANCES IN LEAVES INFECTED WITH RUST

From the foregoing results, it appears that the toxic substances under study are produced in the course of autolysis, and thus one might expect them to be present to some extent in tissues which had been infected with rust, at least where the reaction is one involving the breakdown of host cells.

If we apply the methods described in § IV to rust-infected leaves, and find an active solution produced, it will indicate either that there is a toxic substance present in the living cells, or that some substance present in them is transformed into a toxin by the drying process. Such experiments were made, with these results:

Percentage germination in solutions of the following concentrations (g./l.)

	50	40	25	20	12.5	10	6.25
Rusted leaves	5	—	10	—	30	—	—
	—	0	—	5	—	40	—
	—	—	0	—	1	—	60
	—	—	0	—	5	—	10
	—	—	5	—	40	—	50
Healthy leaves	—	—	30	—	50	—	60

Comparing these results with those cited in the case of the variety Squareheads in the last section, it is evident that these solutions are toxic

to the spores. If, then, rusted leaves contain a toxic (or toxinogenic) substance in the living state, it may be possible to modify this response of the host to the rust by experimental means, in the same way as we can modify the susceptibility to rust attack, for example, by different nutritional treatments. If such control is possible, it should be possible to compare the response of a single variety to rust infection under different treatments, by investigating the amount of toxic substance which the leaves produce. But since the amount of toxin will presumably depend on the actual amount of rust present in a given leaf (apart from the reaction of the host), it is necessary to devise some means of standardizing the leaves in respect of rust content. It so happens that the percentage dry matter of the leaves is modified by rust infection (see Yarwood & Childs, 1938), so that in the ordinary course of drying and weighing the leaves, data are obtained from which an estimate may be made of the amount of rust present in a given leaf. Unfortunately, the differences involved are not large, so that it is impossible to reduce the standard deviation of the determinations below the order of 30 % of the total quantity measured, even when the percentage dry matter of healthy leaves was fixed by the mean of a large number of independent determinations. Notwithstanding this, it seems that this offers the best means of estimating numerically the quantity of rust present, and in view of the consistency of the results obtained it was evidently tolerably reliable in practice within the limits of experimental error. A solution made up using an amount of water = $40.5 \times R \times$ dry weight of the rusted leaf in grams, where R is the difference in percentage dry matter between the rusted leaf and healthy leaves grown in the same conditions (the former being the greater), was said to be of unit concentration, and other solutions were expressed in terms of this standard.

Using this technique, solutions from a series of rust infected plants grown under different nutritional treatments were compared by the methods described above, in respect of toxicity to the spores of *P. glumarum*. The treatments were as follows:

Treatment A: Plants received a complete nutrient "A".

Treatment B: Plants received "A", a solution containing minor elements, "M", and a solution containing boron, "B".

Treatment K: As B but with a solution "K" (containing potassium) instead of "B".

Treatment L: As above, but with a solution "Li" containing Lithium in place of solution "K" or "B".

Treatment M: Controls, receiving "A" and "M", but no other solutions.

Treatment N: Plants received "A", "M", and a solution "N" containing nitrates.

In all treatments the plants were grown in sand containing 99.9 % pure SiO_2 , sterilized immediately before planting, in 6 in. pots standing in earthenware saucers; three such pots were used with each treatment, seven seeds being planted in each pot. At planting all treatments received rain-water up to the capacity of the pots, except treatment L, which received solution "Li". Subsequently the solutions were added at the following intervals:

"A": 6 or 7 times per fortnight

"B": twice per fortnight

"K": 5 times per fortnight

"Li": twice per fortnight

"M": once per fortnight

"N": 5 times per fortnight

On each occasion each pot received 50 c.c. of solution, those receiving no solution getting 50 c.c. of rain-water (the amounts were measured from a measuring cylinder). The solutions used had the following compositions:

Solution "A"	KNO_3	34 g.
	$\text{Ca}(\text{NO}_3)_2$	36 g.
	$\text{Na}_2\text{HPO}_4 \cdot 12\text{H}_2\text{O}$	60 g.
	$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	40 g.
	FeCl_3	4 g.
	H_2O	1000 c.c.
Solution "B"	H_3BO_3	0.6 g.
	H_2O	1000 c.c.
Solution "K"	K_2SO_4	29 g.
	H_2O	1000 c.c.
Solution "Li"	$\text{Li}_3\text{C}_3\text{H}_4\text{OH}(\text{C}'\text{OO})_3$	16.5 g. (lithium citrate)
	H_2O	1000 c.c.
Solution "M"	$\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$	0.1 g.
	$\text{MnSO}_4 \cdot 7\text{H}_2\text{O}$	0.1 g.
	$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$	0.1 g.
	H_3BO_3	0.1 g.
	H_2O	1000 c.c.
Solution "N"	NaNO_3	65 g.
	H_2O	1000 c.c.

All the above solutions were diluted with 99 parts of rain-water before use.

On 14 November, the first leaves of all plants in one pot from each treatment were inoculated with *P. glumarum*. The first toxicity test in the series was carried out on 21 November, and the last on 8 December. The results obtained from this experiment are represented graphically in Graphs I-VI, in which, for each treatment, ordinates represent percentage germination, and abscissae the concentration of the solution in terms of the standard defined above, presented on a logarithmic scale. Each point represents a separate test.

From inspection, it can be seen that all the graphs approximate to falling on the curve

$$b \left\{ 1 - \exp \left[a \left(k - \frac{1}{x} \right) \right] \right\} - y = 0,$$

that for treatment N being the least satisfactory. This equation is not regarded as biologically significant, but was used solely to estimate the significance of the results; assuming that b (the maximum possible germination of the spores used) was 0.9, and that k (the reciprocal of the concentration of solution just sufficient to prevent germination) was 0.67 (it is curious that this quantity was approximately the same for all treatments), a was calculated for each test in which $y > 0$ and $x < 1.5$.

The mean values of a for each treatment (using Common logarithms instead of Natural ones) are given in the following table:

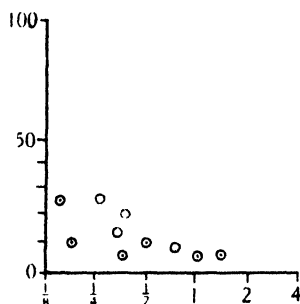
Treatment	Mean value of a	s.d.	s.d. of mean
A	0.038	0.017	0.00615
B	0.192	0.113	0.0565
K	0.049	0.025	0.00944
L	0.156	0.074	0.0302
M	0.303	0.141	0.0814
N	0.150	0.133	0.0502

From these results, it may be shown that the values given for treatments A and K are each significantly below any of the others (taking $P=0.05$ as the criterion of significance), but that they do not differ significantly from each other, nor do any of the other values given. $1/a$ is a measure of the tendency of the leaves to form toxic substances in response to rust attack, and thus it appears that treatments A and K have a greater tendency in this direction than any of the others. Of course, for the reasons given above, particularly the inexactness of the determination of the amount of rust present in a given leaf, the experiment is a very crude one, and with a better technique other and more striking differences might be brought out, but from the present data we can certainly deduce that plants supplied with excess of potassium, or with a deficiency of boron, copper, zinc and manganese, respond to rust infection by a greater production of toxic substances of the type studied than do plants treated otherwise.

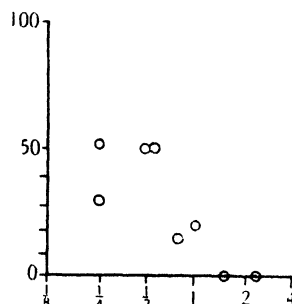
VI. SPECIFIC AND NON-SPECIFIC TOXINS

In the foregoing pages various toxic substances obtained from the wheat plant have been described. They agree in being toxic to the uredospores of one or other of the rusts *P. glumarum* and *P. triticea* in

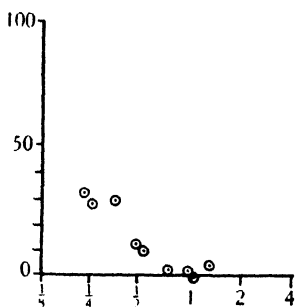
I. Treatment A



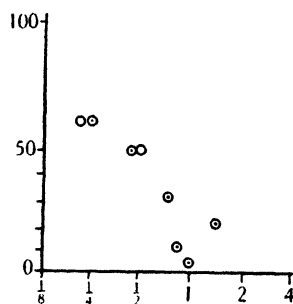
II. Treatment B



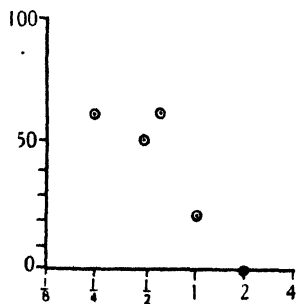
III. Treatment K



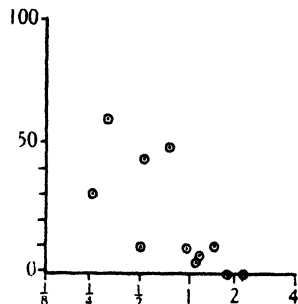
IV. Treatment L



V. Treatment M



VI. Treatment N



Graphs I-VI. In the above graphs, ordinates represent germination percentages observed and abscissae represent the concentration of the germination solution in terms of the arbitrary standard defined in the text.

being stable to temperatures of 100° C., and in being present in the solutions investigated in the same order of magnitude.

Three types have been described: (a) those present in the triturated tissues of wheat plants which have been permitted to undergo some autolysis, (b) those present in leaves undergoing natural decay, and (c) those present in the living state in tissues attacked by rusts. It is reasonable to suppose that these may not all be the same; in the experiments now to be described, it is shown that those produced in rust infected leaves differ in their biological properties from the others, in that they are specific in toxicity for the rust under whose influence they were produced, whereas those of types (a) and (b) appear to affect either species of rust in the same fashion.

The method adopted to investigate this was as follows: plants of various varieties were inoculated either with *P. glumarum* or *P. triticina*; after about a week, until the time of sporulation (in the case of many inoculations of *P. glumarum* this never took place), single leaves were taken from the inoculated plants, making sure that rust was present by the appearance of chlorotic flecks or pale areas on the surface. These leaves were used to prepare solutions by the method used in the nutritional experiments described above, except that no standardization for amount of rust present was attempted. The method of estimating the amount of rust present described above is not likely to give results comparable as between the two species of rust used (compare the accounts of the pathological histology of these rusts given by Allen (1926, 1928)), and since it is exactly this comparison which we desire to make, and since the effect we are looking for is of a qualitative rather than a quantitative nature, it was thought superfluous to attempt any such standardization.

The solutions having been prepared, the activity of those from each species of rust was tested on the uredospores of each species, so that four sets of results were obtained. They were as tabulated hereunder; in preparing the table, it was assumed, on the basis of several calculations on series of figures obtained in this work, that the standard deviation of a single reading of percentage germination was 15 %. Thus, if two readings differ by 30 % or more, they may be regarded as significantly different. In the case of tests made with *P. triticina* spores, the figures were adjusted to correspond to a germination of 60 % in distilled water wherever the actual germination in the control drop was above or below this figure. The figures for tests on *P. glumarum* spores, since no aqueous controls were carried out on this species, were unadjusted. The results were:

Origin of solution: leaves infected with	Tested on spores of	Concentration of solution in g./l. original dry matter	Mean % germina- tion	S.D. of mean %
<i>P. glumarum</i>	<i>P. triticina</i>	24.7	47	5
"	"	12.4	35	10
"	"	6.2	57	10
<i>P. triticina</i>	<i>P. glumarum</i>	24.7	48	10
"	"	12.4	65	12
"	"	6.2	60	10
<i>P. glumarum</i>	<i>P. glumarum</i>	49.4	2	7
"	"	24.7	11	4
"	"	12.4	37	5
"	"	6.2	50	5
<i>P. triticina</i>	<i>P. triticina</i>	24.7	10	12
"	"	12.4	22	10
"	"	6.2	50	12

In all, three readings which were obviously discrepant as compared with others made at the same time have been ignored in calculating the above table.

It is clear from these figures that the solutions were active only upon the spores of the rust under whose influence they were produced, but had no effect appreciable by my methods of experimentation on the spores of the other species. The leaves infected with *P. triticina* were all of the variety Wilhelmina; those infected with *P. glumarum* were of any of the varieties mentioned hitherto, except Little Joss.

It is therefore clear that the toxic substances produced in leaves infected with a given rust are specific for that rust, and in this differ from the toxins which are produced in decaying leaves, and in leaves which have been disorganized by trituration, which affect the uredospores of both species equally. Furthermore, the hypothesis put forward previously that toxins might be produced in rust infected tissues by autolysis consequent upon the breakdown of host cells by the rust, would not appear to be substantiated; rather it would appear that the toxic substances here investigated are in the nature of anti-toxins produced by the host in response to invasion by the parasite. It should however be pointed out that it is possible, as far as the present experiments go, to suppose that the toxins are present in the hyphae of the rust itself, and happen by chance to affect only the spores of the same rust. It is also possible that the specific toxins are in the nature of staling products, though it is scarcely likely that such substances would accumulate without metabolic change in the tissues of a living host, especially in the case of a rust such as *P. triticina*, which, as has been shown by Allen (1926), causes practically no pathological changes in the cells of a compatible host. Further-

more, Porter's work (1924) on the mutual action of fungi through staling products shows that they are definitely non-specific in their action.

VII. GENERAL DISCUSSION

The experiments described in this paper constitute good evidence for the existence of more than one type of toxic substance obtainable from living or dead tissues of the wheat plant, whose toxicity is manifested in the inhibition of germination of uredospores of certain rust fungi. No evidence has yet been forthcoming that this toxicity is extended to other parts of the life cycle of the parasites, though on the basis of one experiment it would appear that germ tubes themselves are also susceptible; a solution, obtained by trituration of fresh tissues, was added to hanging drops in which spores of *P. triticina* had commenced germination for 5 hours in distilled water. The growth of the germ tubes was arrested at this point as compared with the controls. We may reasonably expect, however, that the response of the rust in the living host will not be altogether different from that *in vitro*. We further do not know whether other rusts attacking cereals are also influenced in the same way; in particular, no experiments have been performed on *P. graminis*.

I have, however, made a series of experiments on various unrelated types of plant affected by rust fungi, to determine whether similar effects prevailed. In all these experiments, extracts of the host have been prepared by the method described in § III, i.e. not involving previous drying of the tissues. The results are tabulated below:

Name of plant	Rust on which solutions were tested	% germination in solution	% germination controls
<i>Triticum vulgare</i>	<i>Puccinia triticina</i>	2 (av.)	50 (av.)
<i>T. vulgare</i>	<i>P. glumarum tritici</i>	5 (av.)	—
<i>T. compactum</i>	<i>P. triticina</i>	0	50
<i>T. compactum</i>	<i>Coleosporium senecionis</i> (aecidiospores)	0	1
<i>Lolium perenne</i>	<i>Puccinia coronata lolii</i>	30	0
<i>Poa pratensis</i>	<i>P. triticina</i>	50	50
<i>Phyllostachys virido-glaucescens</i>	<i>P. triticina</i>	0	50 (av.)
<i>Asparagus</i> sp.	<i>P. asparagi</i>	60	100
<i>Salix caerulea</i>	<i>P. triticina</i>	60	50 (av.)
<i>S. viminalis</i>	<i>Melampsora larici-epitea</i>	0	5
<i>Pinus sylvestris</i>	<i>Puccinia triticina</i>	3	85
<i>Selaginella kraussiana</i>	<i>P. triticina</i>	71	84
<i>Hypnum cupressiforme</i>	<i>P. triticina</i>	82	80

From this table nothing of importance can be deduced, except that the toxicity of extracts of plant tissues to rust fungi is by no means universal, whether the rust be one capable of parasitizing the plant in question or not. In view of this it is doubtful whether much significance

can be attached to the occurrence of toxins of this type in the triturated tissues of the wheat plant.

The evidence which leads us to regard the toxins as being produced by autolysis of the host tissues, is however interesting, as it suggests one means by which rust infection may be checked in incompatible hosts. It would however be of interest to know in more detail what particular substances are responsible for the toxic effect, and what relation they bear to the autolysis of the protoplasm in general.

A few experiments were carried out at Cambridge which throw light on this question.¹ Solutions prepared as above were subjected to digestion with enzymes at appropriate acidities and temperatures, and the resulting digests fixed by steaming at 100° C., and readjusted to pH 6.0; the activity of the treated solutions was compared with that of untreated. It was found that trypsin almost completely destroyed the activity, but pepsin did not do so, suggesting that the active substances were of the nature of partially broken down proteins. Further evidence to this effect was obtained by precipitating the ordinary solution with half-saturated ammonium sulphate, and removing the residual proteins from the supernatant liquid by trichloroacetic acid, and redissolving this precipitate, after washing, in water rendered slightly alkaline. The resulting solution had a pH of about 7.0, and germination in it was still significantly inhibited as compared with the controls in distilled water. These experiments were carried out using the uredospores of *P. tritici*.

Thus it would appear that the toxins are the product of protein autolysis, though the above work requires confirmation.

Of more importance is the work which deals with the production of toxic substances in response to rust attack, and in which it is shown that these differ radically from the other toxins in their property of specificity.

As has been pointed out it has not been proved that these substances are analogous to the anti-toxins of animal infections, but this view seems the most likely. The other possibilities are (i) that the toxins are a normal constituent of the rust hyphae, and (ii) that they are secretions analogous to staling products. Both possibilities require experimental investigation, before one can be sure of the interpretation given to the results. How such an investigation might be conducted it is, however, not easy to suggest.

¹ I am indebted to Dr S. G. Dickinson, of the School of Agriculture, Cambridge, for the suggestion that the toxic substances might be proteins.

SUMMARY

A method is described whereby solutions can be obtained from wheat leaves which are toxic to the spores of rusts. Precautions designed to minimize unknown variable factors affecting the activity of the solutions are described.

It was found that the uredospores used germinated better in extracts from Little Joss wheat infected with *Tilletia tritici* than in that from healthy plants, this being correlated with the relative susceptibility of the two kinds of plant under field conditions. On the other hand, no correlation was obtained as between four different varieties tested in the healthy state.

A method is described, by which solutions are obtained in which enzymic activity in the course of preparation is reduced to a minimum. It is found that solutions prepared in this way are non-toxic, if obtained from healthy living leaves, though present in decaying leaves. It is deduced that the toxic substances studied are formed in the course of autolysis.

It is found that, using the second method of preparation, solutions obtained from rusted leaves are toxic. An experiment is described in which modifications of the degree to which such toxins are produced by a given amount of rust infection are brought about by different nutritional treatments, excess of potassium and deficiency of minor elements being conducive to the production of toxins.

Experiments are described which demonstrate that the toxins produced by infection with *Puccinia glumarum* are toxic only to spores of that species, and not to those of *P. triticina*, and *vice versa*.

In the discussion, this last result is especially commented on, and evidence is also brought forward to suggest that the toxic substances first described are in the nature of proteins of light molecular weight; from the fact that they are non-specific, it is clear that they are not of the same nature as the specific toxins produced in response to rust attack. It is suggested that the latter are analogous to the antibodies known in animal pathology, but two alternative hypotheses are also put forward.

In conclusion I would like to express my gratitude to Prof. F. T. Brooks, of the Botany School, Cambridge, and to Prof. B. T. P. Barker, Dr T. Wallace, and Mr L. Ogilvie of the Agricultural and Horticultural Research Station, Long Ashton, for helpful criticism and advice, and for the interest they have shown in my work.

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EXPERIMENTAL METHODS WITH COTTON

II. A STUDY OF THE EFFECTS OF SEED RATE AND TIME OF THINNING ON THE DEVELOPMENT AND YIELD OF COTTON PLANTS IN HAND-PLANTED COTTON TRIALS

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(With Plate III and One Text-figure)

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INTRODUCTION

IN the planting of cotton variety and other trials on the Cotton Experiment Station, Barberton, it has been customary to use three acid-treated, water-sinking seeds per hill as the normal seed rate. It was often noticed that where a larger number of seeds had been planted, accidentally, on any one hill, the seedlings appeared to develop more rapidly than where only three seeds had been planted. Development of the cotton plant on the loam soil of the Station is generally slow in the early stages, and it was important to find out whether, by increasing the seed rate, early growth and general development could be speeded up, thus shortening the period over which the plant is particularly liable to damage.

It was also desirable to determine what effect any such acceleration of early growth would have on final yield. A further point of interest arose from the probability that the effect of the number of seeds per hill would be closely connected with the time of thinning.

MATERIAL

Trials designed to throw light on the above points were carried out during 1936-7 and 1937-8. In both seasons the strain planted was 052, the U. 4 derivative which has been in general cultivation in the district for several seasons. The seed was acid-treated, with the removal of all water-floaters, in the usual manner.

1936-7 experiment. Four treatments, two, three, six and ten seeds per hill, were laid out in randomized blocks, using two-row plots, 90 ft. in length. Each treatment was replicated fourteen times, and the spacings were 3 ft. 6 in. between rows and 2 ft. between plants in the row. A portion of each plot length was thinned at the growth-stage at which thinning is normally done, and used for final yield figures. The remaining portion was used for plant weight sampling and development studies under three times of thinning treatments—early, medium and late.

1937-8 experiment. The design was modified in order to make possible a study of the combined effect of number of seeds per hill and time of thinning on ultimate yield. The number of treatments was increased to twelve, making provision for an early, medium and late thinning on a complete plot of each seed-number treatment, instead of on sample plants only as in the previous season. It was thus possible to carry out a detailed study of general plant development, for each of the twelve treatments, throughout the season, from germination to final yield.

Again two-row plots were used, but their length was doubled, experiments on plot shape having proved the value of ultra-long and narrow plots under Barberton conditions. The increase in treatment number from four to twelve necessitated reduction in the number of replications from fourteen to seven. The centre portion only of each plot was used for final yield, small portions at each end being reserved for sampling after thinning had taken place.

The spacing was altered to 3 ft. both between rows and between plants in the row. This spacing was in general use over the whole experimental area for this season in order to admit of cultivation on the contour. It has since been discontinued for a number of reasons.

In the first season excellent conditions prevailed for several months

after planting, growth was good and a crop of 942 lb. of seed cotton per acre was harvested.

In the second season planting was late and heavy rains kept the soil very wet during the following month. Growth was slow, as will be seen by comparing the figures for the two seasons, and the crop was cut off prematurely by a severe drought late in the season, the final yield averaging only 290 lb. of seed cotton per acre for the twelve treatments.

EXPERIMENTAL DATA

(1) *Stand*

The 1936-7 trial was planted on 17 November, while the 1937-8 trial was put in on 2 December, planting and germination conditions for both being very good. Stand counts were made in the first season on three occasions, but in the second season such high percentages were recorded at the second count that a third was considered unnecessary. In counting, the presence of a single germinated seedling was taken as unit germination for that hill; no attempt was made to record the number of seeds which germinated per clump. The figures are given in Table I, together with final counts made at the time of harvesting.

Table I. *Stand counts at germination and harvest (percentages)*

No. of seeds per hill	1936-7				1937-8		
	6 days	8 days	14 days	Harvest	6 days	8 days	Harvest
10	93.3	97.5	98.9	96.9	95.9	99.6	92.5
6	88.8	96.3	98.9	95.8	91.7	98.8	93.8
3	81.5	90.8	95.2	92.5	85.1	98.6	91.7
2	75.3	87.6	91.0	87.7	75.7	95.1	90.0
$P=0.05$	5.5	3.4	2.4	2.9	3.8	1.2	1.9

As would be expected, the higher seed rates gave considerably better stands in the earlier counts, and though the lower seed rates caught up to a certain extent later, the final stands were still in favour of the higher seed rates. On both occasions two seeds gave a definitely sparser stand than the other three treatments, but there appears to be little advantage in planting more than three seeds per hill.

Counts at harvest showed a slightly greater mortality in the second year than the first, but in neither season was there any significant difference in mortality between treatments.

(2) *Plant height and weight*

In both seasons a series of samples for green weights, together with a series of plant height measurements made concurrently with the former

provided plant development data during the first two to two and a half months of growth. Subsequent development was recorded during the main fruiting period by daily flower counts, described in § 3.

Under the general heading above it is proposed to deal separately with the plant height and weight data, combining the two in a third subsection in the form of height-weight ratios.

Sampling for both weight and height was on a random basis, the sample amounting to approximately 5 % of the population. When sampling prior to thinning, the number of seedlings in the sample clumps were always counted to ensure that the correct number of seedlings were present, as for instance, the failure of one seed to germinate in a three-seed treatment hill would make that particular hill comparable with a two-seed treatment hill. In such cases, which were comparatively rare, the nearest hill in the row with the correct number of seedlings was taken.

As no provision had been made in the 1936-7 experiment for varying dates of thinning on complete plots, the area set aside for sampling was utilized to provide three times of thinning treatments on sample hills of each seed-number treatment.

At the date of the first sampling the clumps thus selected were thinned to one plant per hill, after plants had been taken from each clump for green weights, to represent the early thinning treatment. The same procedure was adopted at the second and third dates of thinning.

(a) *Plant height.*

In both experiments height measurements were made on unthinned plants at three different dates, corresponding to the three times of thinning. The height recorded was from the cotyledonary node to the apical bud in both cases, while in the second year the height from ground level in cotyledonary node was also recorded.

The heights given in Table II were all made on plants from unthinned hills.

Table II. *Heights of unthinned plants in centimetres.*
Cotyledonary node to apical bud

No. of seeds per hill	Age when measured						Height ground level to cot. node at 20 days
	31 days	41 days 1936-7	55 days	20 days	43 days 1937-8	54 days	
10	10.6	20.4	34.1	1.4	12.4	20.1	7.5
6	10.5	18.5	35.3	1.8	12.2	24.0	6.9
3	9.6	18.0	33.1	1.8	12.4	21.9	5.1
2	8.5	16.0	30.7	1.4	11.1	20.9	4.6
<i>P</i> = 0.05	0.7	1.3	2.4	0.3	Insign.	2.6	0.7

In the figures for 1937-8 the effect of increasing seed rate on the growth of the stem below the cotyledonary node is very evident; any increase in seed number causing the hypocotyl to elongate rapidly. Measurements from ground level to cotyledonary node were also made at 43 and 54 days, and these were, as would be expected, almost identical with the measurements given for 20 days.

For heights above the cotyledonary node the connexion between seed numbers and heights is not so simple. In the 1936-7 season, when growth was good, the figures for the first two occasions show definitely that increasing seed number caused increasing elongation of the stem. In the 1937-8 season growth was very poor and such effect was not apparent. In both seasons, however, there is evidence that, at a later stage, with ten seeds per hill, the elongating effect of crowding the plants together is more than counteracted by the retarding effect of competition, probably for moisture or nutrient. In the 1936-7 season, between 41 and 55 days from planting, the percentage increases in height were 67 % for the ten-seed treatment and 91 % for the six-seed treatment. In the second season the corresponding figures were 62 % and 97 % respectively.

In both seasons, at the date of the last thinning, sample plants from the early and medium thinned treatments were remeasured. A further measurement of all twelve treatments took place at 72 days in 1936-7, and at 70 days in 1937-8. Figures for all these measurements on thinned plants are given in Table III.

Table III. *Heights of thinned plants in centimetres.*
Cotyledonary node to apical bud

1936-7								
No. of seeds	Heights at 55 days Age when thinned			Heights at 72 days Age when thinned				
	31 days	41 days	55 days	31 days	41 days	55 days		
10	26.9	29.3	34.1	42.7	45.4	47.4		
6	27.4	28.4	35.3	44.8	44.1	50.2		
3	29.1	30.4	33.1	48.4	48.4	49.6		
2	26.6	28.4	30.7	45.3	45.7	48.0		
$P=0.05$	Insign.	Insign.	2.4	3.1	Insign.	Insign.		

1937-8								
No. of seeds per hill	Heights at 54 days Age when thinned			Heights at 70 days Age when thinned				
	20 days	43 days	54 days	20 days	43 days	54 days		
10	16.1	18.4	20.1	31.7	32.2	32.8		
6	18.5	19.1	24.0	32.3	32.8	35.4		
3	20.8	18.9	21.9	35.0	35.4	35.3		
2	19.5	18.9	20.9	35.6	33.6	35.8		
$P=0.05$	2.6			Insignificant				

The most noticeable point in Table III is the rapid elongation of the stem that takes place when thinning is delayed. This elongation is considerably more marked in the case of the larger seed rates than in the smaller.

The initial elongation in stem height caused by high seed rates (Table II) is stopped when thinning takes place, plants from the smaller seed rates catching up and eventually surpassing plants from the larger seed rates.

(b) *Plant weight.*

Samples for green weights in both seasons were taken on the same dates as height measurements. In 1936-7, however, the design of the experiment did not allow the effect of time of thinning to be carried through to flowering and final yield, as the sample plants for all three times of thinning were pulled up for green-weight determinations at 72 days from planting.

In the case of both experiments dry-weight determinations were made at each sampling. They revealed only infinitesimal differences in moisture content between the treatments, however, and for this reason green weights only are given in the figures that follow.

The figures in Table IV refer to green weights of plants from unthinned hills. In all cases the plants were pulled up, the taproot therefore being included in the plant weight figures.

Table IV. *Green weights of unthinned plants in grams*

No. of seeds per hill	1936-7 Age when weighed			1937-8 Age when weighed		
	31 days	41 days	55 days	20 days	43 days	54 days
10	4.8	14.4	50.3	1.7	5.2	15.3
6	4.8	16.0	57.0	1.9	6.7	24.4
3	4.9	17.5	68.4	2.0	9.3	30.0
2	4.9	16.0	59.1	1.8	8.4	26.6
$P = 0.05$	Insign.	Insign.	11.9	0.2	2.6	10.6

It can be seen from Table IV that in the first sampling, in both seasons, there is comparatively little difference between the weights of plants from any of the four seed rates. It must be remembered, however, that at this stage there were big differences in height measurements between the treatments. As thinning is delayed, and competition between the plants becomes more acute, the effect of the number of plants per hill becomes much more marked. Thus, in both seasons, the weights at the later dates increase regularly and markedly with reduction of

seed rate from ten to six to three. In both experiments, however, the two-seed treatment gives lower weights than the three, though this difference is in no case significant.

Green weights of thinned plants are given in Table V, on one occasion in 1936-7 and on two occasions in 1937-8, when a whole plot of each thinning treatment was available.

Table V. *Green weight of thinned plants in grams*

		1936-7					
		Weights at 72 days					
		Age when thinned					
No. of seeds per hill		31 days	41 days	55 days			
	10	198.8	187.6	155.2			
	6	199.4	184.7	174.9			
	3	240.3	236.4	200.2			
	2	222.3	226.4	192.4			
$P = 0.05$		24.0	29.8	25.7			
1937-8							
		Weights at 54 days			Weights at 70 days		
		Age when thinned			Age when thinned		
No. of seeds per hill		20 days	43 days	54 days	20 days	43 days	54 days
	10	30.2	29.4	15.3	141.1	127.2	104.3
	6	40.8	29.3	24.4	148.3	135.3	119.4
	3	39.2	36.5	30.0	166.5	168.9	126.9
	2	42.6	38.0	26.6	178.6	127.4	141.0
$P = 0.05$		10.6			42.4		

In Table V the deleterious effects of increased seed rate and delayed thinning are very obvious. As with plant heights, the differences between times of thinning are greater with the larger than with the smaller seed rates.

Another interesting point is the apparent permanence of the seed-number effect, at least up to 7 weeks from thinning. At 70 days from planting, early thinned plants from the two- and three-seed treatments were considerably heavier than early thinned plants from the six- and ten-seed treatments.

In spite of taking 5 % samples the figures show some irregularity, notably the medium thinned two-seed treatment at 70 days, which, judged by earlier and later figures is probably considerably below the real figure for this treatment. The occasional discrepancies, however, do not destroy the general sequence of results.

(c) *Height-weight ratios.*

The height and weight data examined in the previous sections were combined to form height-weight ratios. The ratios so formed can be

regarded as a measure of the lateral development of the plants, in so far as they represent weight per unit length of stem.

The data used were the heights and green weights recorded at 72 and 70 days from planting for the 1936-7 and 1937-8 experiments respectively. In the first year's experiment height is from the cotyledonary node to the apical bud only, whilst in the second year height is from ground level to apical bud. Had the hypocotyl been included in the first year's figures the differences between the seed-number treatments would have been even greater than those shown in Table VI.

The height-weight ratios, for both experiments, are given in Table VI, in the form of weight per unit length of stem.

Table VI. *Weight in grams per centimetre of height*

No. of seeds per hill	1936-7 Age when thinned			1937-8 Age when thinned		
	31 days	41 days	55 days	20 days	43 days	54 days
10	4.66	4.13	3.27	3.60	3.16	2.59
6	4.45	4.19	3.48	3.79	3.39	2.82
3	4.97	4.89	4.04	4.16	4.11	3.10
2	4.91	4.96	4.01	4.44	3.31	3.46

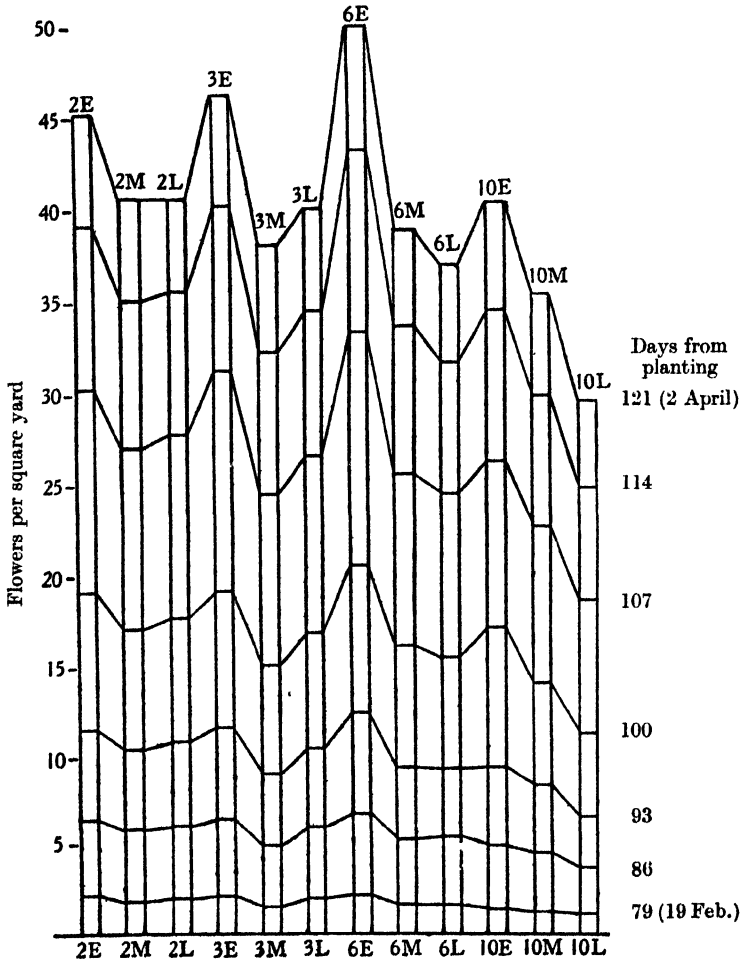
There is a general sequence in the figures, showing a falling off in weight per unit of height from early to late thinning, and with increments of seed number planted per hill. The ten- and six-seed treatments, thinned late, are at a very distinct disadvantage.

In the 1937-8 experiment the first thinning, at 20 days, was at a much earlier date than has been usual on the station, but even with this very early thinning the plants from the larger clusters do not thicken out to the same extent as plants from the smaller clusters. Thus, 7 weeks after thinning, there is still a 20 % difference in height-weight ratio in favour of the early thinned two-seed treatment over the early thinned ten-seed treatment.

The big differences in height and weight between plants from hills with varying numbers of seeds raises an interesting point in the early sampling of any cotton trial. When sampling before thinning, it would seem advisable, in view of these figures, to take the sample plants from hills with the same number of seedlings in them, in order to reduce the sampling error.

Taking into consideration both plant height and plant weight data, and especially the ratios of height to weight, it is very obvious that the planting of large clumps of seed does not give the young cotton plant a better start in life, but rather the reverse. It is clear that the visual

appearance of better growth in larger clumps is due to the fact that the plants are drawn up more and that the greatest number of plants masks their lack of sturdiness.



Text-fig. 1. Histogram depicting flowering, 1937-8. (E, M and L refer to thinning at 20, 43 and 54 days from planting.)

The photographs in Plate III, taken soon after the date of the last sampling for green weight in the season 1937-8, illustrate very clearly the differences in general plant development caused by different seed rates and times of thinning.

(3) *Flower counts*

Daily flower counts were made on both experiments, but as the plot layout in 1936-7 did not allow for the study of time of thinning to be carried on after 72 days, flower count and final yield figures are only given for the 1937-8 experiment. Counts were not made on Sundays, but the data presented in histographic form in Text-fig. 1 have been adjusted to represent "flowers per square yard per week", the week being a full one of 7 days. By quoting the flowering rate on an area basis instead of per plant any advantage due to a better stand from a higher seed rate has been allowed to exert its effects on the figures.

In Text-fig. 1 the most striking feature is the beneficial effect of early thinning compared with medium and late, with all four seed rates. Comparing the effects of seed rates, ten seeds per hill shows up as being definitely harmful, even when thinning takes place early. The slight stand advantage produced by planting ten seeds per hill, compared with two, does not counteract the bad effect of the high seed rate on the early growth of the individual plant.

(4) *Final yield*

Final yield figures for 1937-8 are given in Table VII. The yields are expressed as percentages for convenience in comparison, and it should be noted that these calculations were made on seed-cotton data, ginning percentages not being taken into account as there were no differences between treatments in this respect.

Table VII. 1937-8, *final yields, expressed as percentages of the early thinned, two seeds per hill treatment*

No. of seeds per hill	Age when thinned		
	20 days	43 days	54 days
10	87	80	73
6	105	94	89
3	104	93	95
2	100	100	99

$P=0.05$

11

In Table VII the ten-seed treatment, at all times of thinning, is shown to be definitely harmful, while the two-seed treatment is slightly below the three-seed and six-seed treatments when thinned early, probably because of stand differences. With later thinnings the poorer stand of the two-seed treatment is more than compensated for by the better

development of plants from these hills in comparison with plants from larger hills.

The three-seed and six-seed treatments show comparatively little difference in yield when thinned early, but the six-seed treatment falls off more rapidly when thinning is delayed.

The importance of early thinning, particularly with the higher seed rates, is brought out very clearly in Table VII. This point in favour of the lower seed rates may be of importance in some years, when unfavourable weather conditions or other reasons cause thinning to be delayed longer than is desirable. It appears, therefore, that a seed rate of three seeds per hill should be most satisfactory.

The difference in yield between the three-seed and ten-seed treatments, thinned early, should be noted. It is remarkable that this difference, amounting to 17 %, has been brought about entirely by conditions governing the life of the plant in the first 20 days of growth, conditions for the remaining 182 days being identical for both treatments.

DISCUSSION AND SUMMARY

The object of this experiment was, in the first place, to see whether, with cotton experiments, there was an advantage in planting a larger number of seeds per hill than the customary number of three; and, in the second place, to see the effect of the interaction of time of thinning with varying numbers of seeds per hill.

In cotton breeding work, where trials of new strains have to be carried out as soon as sufficient seed is available, it is important to conserve seed in all possible ways. At the same time it is necessary to plant sufficient seed to give a full and even stand for all strains.

In experiments carried out in 1936-7 and 1937-8 stand counts, made soon after germination, showed the advantage of the higher seed rates in obtaining a quick and full stand. Later counts and final counts at harvest showed a considerable evening up, although the two-seed treatment proved unreliable, giving the lowest stand in both seasons.

Plant height and weight records, made during both seasons, showed that plants from the larger hills were drawn up much more rapidly than plants from the smaller hills. This rapid elongation in stem height proved, from weight figures, to be at the expense of lateral development, weak and leggy plants being produced in these hills. The ten-seed treatment showed up particularly badly in this respect, the yield figures showing that the plants never recovered from this early deleterious effect.

The six-seed treatment, whilst giving a quick and excellent stand suffered to a certain extent from the same defects as the ten-seed treatment. If thinned early they tended to fill out and become more comparable with plants from the three-seed treatment, but when thinning was delayed they never caught up and final yield suffered adversely.

In both years the three-seed treatment proved the most reliable, its stand being very little inferior to that produced by the six-seed and ten-seed treatments. Before thinning the two extra seedlings were not sufficient to cause any very marked elongation in stem height, or to retard general development through competition. The seedlings were strong and well developed and were able to go ahead alone after thinning with a good basis on which to build their fruiting structure.

With reference to time of thinning, early thinning was shown to be an advantage with all seed rates, but especially so where large numbers of seeds were planted. Any delay in time of thinning is liable to be much more harmful where six or ten seeds are planted, than where only two or three seeds are planted. This greater latitude in time of thinning with a smaller number of seeds is a point decidedly in their favour, as the actual time of thinning may easily be delayed for a week or 10 days longer than desirable through unfavourable weather conditions or other circumstances.

Results from the two years' experiments indicate, therefore, that there is no advantage, when using acid-treated, water-sinking seed, in planting more than three seeds per hill.

An interesting point is the effect of delayed thinning on the structure of the plant. It has been observed that there is a general absence of lateral branches on that side of the plant which faces its neighbour or neighbours in any one hill. If thinning is left too long this effect may become permanent and produce a lop-sided plant, particularly where a large number of seeds has been planted in one hill. The photograph in Plate III (*b*) shows this lop-sided development in the case of a plant from a late-thinned bunch of ten.

The early and permanent adverse effect on the development of the individual plant of planting large numbers of seeds, or of delay in thinning, becomes of particular importance when the question of single-plant selection arises. Where such work is being carried out it is essential that all the plants should have as equal a chance as possible. In this work, therefore, it is of special importance that planting should be carefully supervised to prevent large bunches, and that thinning should take place early. Where a larger number of seeds than three is planted,

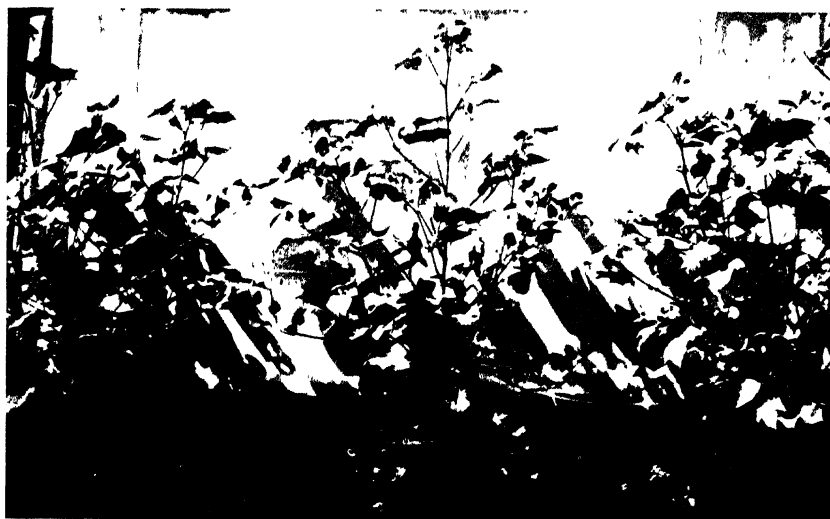
either accidentally or otherwise, it is recommended that the hills should be thinned down to three at a very early stage, and later thinned down to one.

This is now a practice at Barberton with cotton experiments as well as with breeding plots, as the accidental occurrence of large clumps is a probable source of error in sampling for green weights and heights, especially in the early stages of growth.

ACKNOWLEDGEMENT

The authors wish to express their indebtedness to Mr F. R. Parnell, under whose general direction this work has been carried out, and whose advice and criticism throughout have been invaluable.

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(a) Typical plants, well balanced and with good lateral development,
from early-thinned bunches of three seedlings



(b) Typical plants, less well balanced and with poor lateral development,
from late-thinned bunches of ten seedlings.

A STUDY OF THE METABOLISM OF FOWLS

I. A CALORIMETER FOR THE DIRECT DETERMINATION OF THE METABOLISM OF FOWLS

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(With Nine Text-figures)

SOME years ago my colleague, Mr E. T. Halnan, suggested the construction of the present instrument for the purpose of determining figures for domestic fowls corresponding to those of Kellner for ruminants.

Owing to the activity of the fowl, it is essential that an instrument for this purpose should be capable of recording accurately a heat output which may be varying with some rapidity.

From this point of view the advantages of the indirect method were considered but were eventually rejected for the following reasons: (a) the advantage accruing from our greater experience of the direct method in this laboratory, (b) the work of Adams & Poulton (1933, 1934, 1935) calling in question the fundamental bases of the indirect method, and (c) the very variable R.Q.'s obtained in earlier work by numerous investigators working with birds.

That the decision was wise soon became apparent when work on birds was begun. It is certain that no ordinary apparatus of that kind could possibly take account of the variations caused by the constant changes in activity.

The principle of a "compensatory" or "balanced" calorimeter more or less as developed by Noyons (1927), Benedict (1927) and Heyster (1933), was selected as the most likely to give promptness in registration, and this choice has been amply justified in the result. Such instruments can be very lightly constructed, although where living animals are concerned, since their movements cannot be controlled, as can those of a human being, a greater margin of strength has to be provided, which naturally increases the heat capacity and lag and reduces sensitivity to small changes in heat evolution.

The calorimeter as finally constructed consists of two chambers of similar construction supported on a wooden framework at a suitable

height for easy operation. In one the fowl is placed and the other contains a heating element and a means of regulating the water vapour. The air in both is stirred at a constant speed while the ventilation is kept equal by a rotameter. Hair hygrometers serve for rough adjustment of water vapour during the experiment, the final determinations being made in each case by a chemical hygrometer. The temperature is adjusted to equality in the two chambers by varying the current in the heating element so as to maintain zero deflexion on a galvanometer connected in a Wheatstone's network, across fine wire grids in the sides and top of the chambers. The covers are made so as to be raised for admission of the bird, etc. and drop into a mercury trough in the base forming an airtight luted joint. The main lines of the construction are seen from Fig. 1, which shows only one of the chambers.

Covers. A copper framework was first made for the covers on a rectangular base 2 ft. 4 in. \times 1 ft. 11 in. and 2 ft. 3 in. high. It was made of $\frac{3}{4}$ in. angle copper of 20 B.W.G. (35 B.W.G. was first tried but proved too light); this had to be made in the laboratory and a difficulty was the bowing of the pieces after removal from the cramp. It was found possible to straighten them by judicious fullering of the inside angle. The ends of the angle strips were then mitred and brazed after which the corners were strengthened with riveted and soldered caps of 27 B.W.G. copper. When the framework had been completed in this manner it was found that some of the angles were slightly out of truth, and this was rectified by melting the solder used for the caps at two opposite corners of the rectangle while maintaining a cross tension between the other two corners. The quadrangle forming the base of the covers was originally made of the same gauge copper as the angle strips, but this was found to be insufficiently rigid and a piece of brass strip $1\frac{1}{2} \times \frac{1}{8}$ in. was substituted. Throughout the construction each part of each cover was weighed against the corresponding part of the other and the same with each partially assembled portion of the whole. A tolerance of one-half of 1 % was allowed in all cases.

To provide for the suspension of the covers two welded iron supports were procured (Fig. 2) so designed that the suspension point could be varied somewhat to allow of the covers hanging straight when supported from one point only. These were bolted to the angle copper strips forming the longer sides of the top.

For the walls of the covers celluloid sheet $\frac{1}{16}$ in. thick was used; it is light, its thermal conductivity is not too great, it is harmless to birds and is an insulator as far as electricity is concerned; which last fact

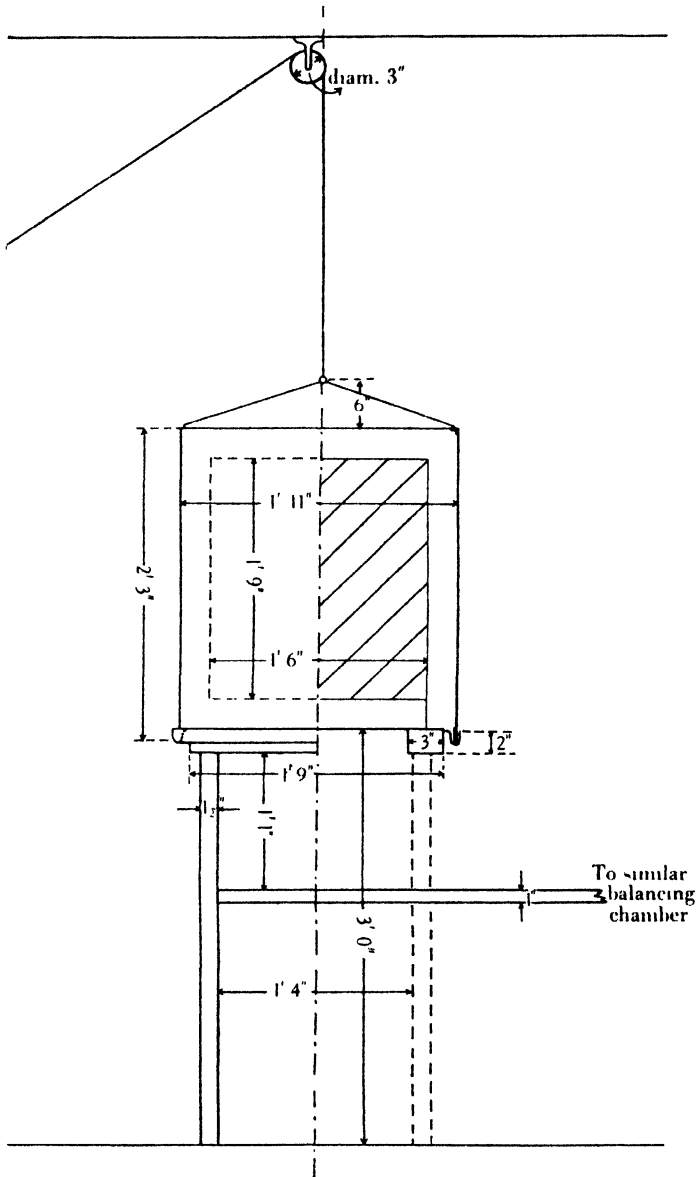


Fig. 1. Poultry calorimeter. Front elevation. All subsidiary apparatus omitted. Scale $\frac{1}{2}$ in. to a foot.

simplified the fixing of the wire nets for use as resistance thermometers in equalizing the temperatures of the two chambers. Furthermore, it is transparent, allowing the fowls to be under continuous observation while an experiment is in progress. The weight of these celluloid windows and the bolometers was taken by thin angle strips of copper $\frac{1}{4} \times \frac{1}{4}$ in. soldered on the inside of the bottom copper band of the frame, while the windows

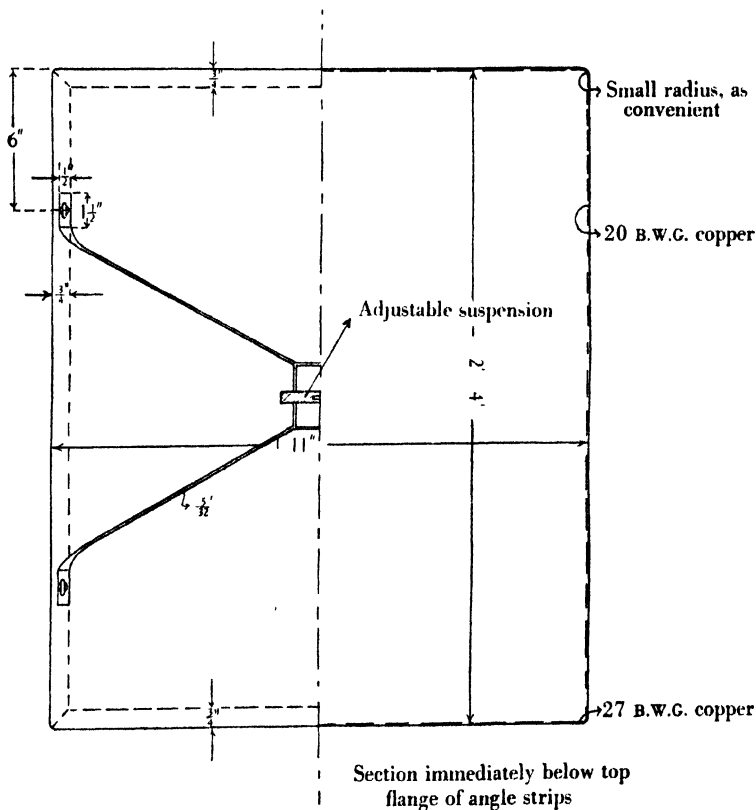



Fig. 2. Poultry calorimeter covers and support. Plan. Scale $1\frac{1}{2}$ in. to a foot.

were fixed to the copper strips by a celluloid cement. This proved somewhat inadequate after a time and the windows were eventually bolted on to the copper angle strips of the framework by $\frac{1}{8}$ in. bolts through thin brass strips placed on the inside of the windows. The celluloid cement was then discarded in favour of a vacuum wax which proved satisfactory.

Later it was found to be desirable to divide each large window into

two parts by a copper strip running horizontally half-way up the height of the cover.

When the completed covers were tested on the metal tray to be described later, it was found that the heat insulation of the single layer of celluloid was insufficient even when the tray was insulated with felt, since an insufficient temperature rise of the inside air was registered with a heater generating heat equal to that of a small fowl. It was therefore decided to increase the insulation of the wall by fixing air cells of celluloid on the outside of the covers. To avoid buckling and such-like troubles in fixing these a thinner grade of celluloid sheet (10 mils.) was used, separated from the original wall by $\frac{1}{4}$ in., and the intervening space was divided into cells about 7×4 in. by celluloid strips bent thus . These were affixed to the inner wall and the outer wall stuck on to them by celluloid cement made up by dissolving celluloid scrap in amyl acetate which remains wet sufficiently long for the completion of the work. In this way, and with the tray insulated, a sufficient temperature rise was obtained.

The final weights of the completed covers were

Cover no. 1 6785 g.

Cover no. 2 6825 g.

Both the covers were then tested for airtightness and were not passed until each was capable of retaining a pressure in either direction of 45 mm. of water unchanged for 12 hr. This was about three or four times what they are required to sustain in an experiment.

Some delay was caused by the vapour of the amyl acetate cement causing permanent clouding of the celluloid so that it became semi-opaque. Microscopic examination showed that this was due to swelling of minute furrows on the surface and avoided by replacing the parts affected with very highly polished sheets specially supplied by the British Xylonite Co.

The covers are suspended from pulleys on the ceiling of the room as shown in Fig. 1, and to prevent them rotating when raised while avoiding the complication of fixing guide bars at the corners a cord is run over the top at each side falling down at each end and running under pulleys of the third order raising weights as the cover is raised. In this way the cover is kept square to the tray and the cords can be moved sideways if desired for the insertion of the cages.

Base plates. The design of the base plates is shown in plan and section in Fig. 3 and consists essentially of a copper plate surrounded

by a mercury trench and provided with a depression for the fan vanes, pierced in the centre for admission of the fan spindle from below, and with holes as required for admission of inlet and outlet ventilating pipes, terminals, etc.

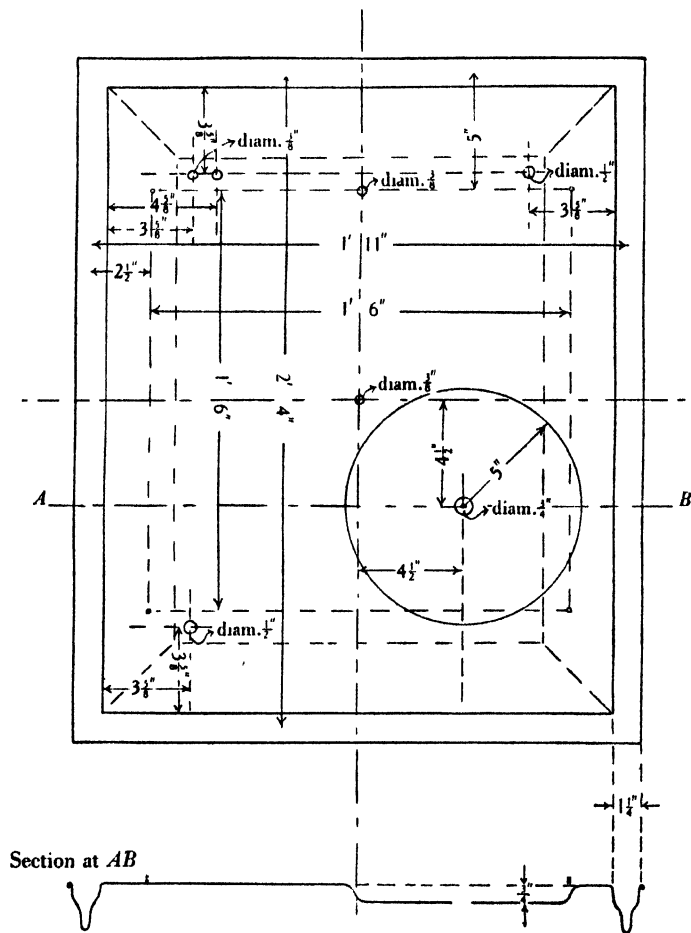


Fig. 3. Poultry calorimeter. Base plate. Scale $1\frac{1}{2}$ in. to a foot.

Much trouble was experienced in rendering the mercury trenches sound. Four coats of copal varnish, and later a thick coating of vacuum wax proved quite incapable of rendering them mercury tight for longer than about a week. After this the mercury began to attack the solder at the joints and soon ran through. This difficulty was satisfactorily

overcome by having the corner joints brazed up and then having the whole tray nickel plated. A coat of vacuum wax was then given to the inside of the trenches and they have now remained full of mercury for several years without mishap. For a similar reason it was found necessary to have the bottom $\frac{1}{8}$ in. copper strip forming the bottom rectangle of the covers nickel plated and varnished.

As regards the rather peculiar sectional shape of the mercury trench, this was decided on with two objects in view: (a) the mercury seal must be deep enough when displaced by pressure and suction to allow of testing the covers and trays under increased and reduced pressure and (b) the trench must be of such form that there cannot be any doubt as to the perfect covering of its sides with vacuum wax.

The heat insulation of the trays is effected by covering them above and below with $\frac{1}{4}$ in. "Onazote" expanded rubber, and making the lead in and outlet tubes for the ventilating air of fibre instead of metal. No such method was available in the case of the fan spindle and the terminals but these are both thin and the onazote is brought well up to them all round. No difficulty has been experienced on account of heat leakage at these points.

Internal air mixing fans. The rendering of the fan spindles airtight was a more difficult matter. The general precautions in this regard and the mode of operation are shown in Fig. 4. The two concentric cylinders are of nickel plated brass and the bottom of the outer cylinder which rotates with the shaft is partly filled with mercury to a depth sufficient to form a sealed joint which remains sound when the fans are rotating at full speed and a positive or negative pressure in excess of the maximum experimental requirement is maintained in the chambers. The fans are run from a single shaft driven by a small motor through similar gear trains and consequently the stirring of the air in each chamber remains the same at all times. The fan vanes are attached above the plate *AB* in the figure, which represents a section of the bottom of the depression in the copper base plate of the chambers. Other details will be clear from the sketch.

Tests showed that friction at the bearing where the fan spindles pass through the base plate was not sufficiently great to produce any measurable quantity of heat.

Internal cages, etc. Cages were made to fit inside the covers to accommodate the bird and to prevent it from access to the resistance wires by beak or claw. To balance the heat capacity of this a similar one had of course to be made for the compensation chamber. The

framework of these cages is of $\frac{1}{8}$ in. steel rod with insulated feet fitting into sockets on the base plate of the chamber. These frames are covered with fine wire netting and the cage is provided with a wire netting screen inside to protect the fan vanes. Each has a door of such size as is necessary for the admission of the bird or compensating apparatus as the case may be. A perch is provided in the cage in which the hen is placed, its heat capacity being approximately balanced by that of a few pieces of apparatus in the compensation chamber.

Ventilation. Air is admitted to the chambers by a copper tube attached to the fibre tube used for the passage of the inlet air through the base plate. This passes to the top of the chamber and the air comes in through a rose nozzle. On leaving the chamber the air passes through an air filter before passing to the electrically driven exhaust pump used for maintaining the flow of air. This flow is regulated by taps controlled by screw and spring mechanisms placed in the tubes leading from the chambers to the pump; thus any difference which may exist in the resistance to air flow due to the air filters does not affect the working of the apparatus. After passing through the pump the air is carried away into a flue. The inlet air is actually taken from the room, but if indirect apparatus is afterwards added, there will be no difficulty in supplying outdoor air to the chambers. At present, room air is taken in over CaCl_2 , cooled by passing through metal spirals to get rid of the heat generated in the process of drying which is quite considerable, and then passed through two parallel rotameters one for each chamber. After this the air on its way to the chambers passes through two metal spirals wound together and kept away from draughts so that the temperature of the air actually delivered to the two chambers may be the same, and from these the air passes to the inlets by as short a path as possible.

Clearly the greater the flow of air through the instrument the less will its sensitivity be. On the other hand, a lower limit is placed on the flow by the necessity of keeping the composition of the air at the close of an experiment at all events less than 1% CO_2 . The volume of each chamber is 273 l., while the CO_2 production of a large fowl does not exceed about $1\frac{1}{2}$ l. per hour; hence allowing for the ventilation given the CO_2 would only exceptionally exceed 1% at the end of 3 hr., which is the normal time occupied in an experiment. We may say then that it will at all events be justifiable to use air flows down to 1 l. per minute and in most cases even less. Normally a flow of 1.7 l. per minute has been employed.

Wire resistances and terminals. The wire resistance nets used for

maintaining temperature equality in the two chambers were originally made of 36 s.w.g. bare copper wire but experience showed that these were too fine as they were liable to get broken or twisted up in the process of raising and lowering the covers, removing the cages or screwing up the terminals or even by the draught caused by the stirring of the air inside the chambers. 34 s.w.g. wire was therefore substituted, the battery and galvanometer were interchanged in the Wheatstone network so that the same sensitivity was obtained, and this has proved quite satisfactory. Pure nickel wire might be used with advantage as was done by Noyons but this proved difficult to obtain of a sufficient degree of purity and a very small admixture of foreign matter is sufficient to reduce the temperature coefficient of resistance to a marked extent; also thermoelectric difficulties would have to be guarded against.

The wire nets are threaded through ebonite bars fixed on to the terminals and the weight of these and of the terminals is supported by the celluloid windows.

A terminal had to be designed which would be airtight and yet adjustable, as it was not certain at first what would be a satisfactory distance to allow between the windows themselves and the resistance nets. How this was accomplished is shown in Figs. 5 and 6. Fig. 5 shows the way in which the celluloid was prepared for the reception of the terminals (these were fixed in position before the insulating air cells were added). Fig. 6 shows details of the construction of the terminals, the stippled parts being ebonite or fibre insulation and the rest brass. The inner rod slides in the tube passing through the window into another tube on the other side and allows adjustment of the distance of the $\frac{1}{8}$ in. ebonite supporting strip shown at the bottom. It can be fixed in position by the sunk grub screw (see section at bottom), while the terminal is rendered airtight by screwing up the cap against the fibre washer on the outside. Electrical connexion is made from the top terminal by way of the cap to the screwed tube and through that and the grub screw to the adjustable rod carrying the wire net terminal at the bottom.

The tests for airtightness of the covers previously mentioned were made with all the terminals and wire nets in position and with all the air tubes and mica-insulated electric leads through the base plate fixed. The air filters, where the air passes out of the chambers, are filled with oiled fibre.

Bridge and vapour compensator. The remainder of the Wheatstone's network was completed, apart from the 2 V. accumulator and leads, by manganin resistance coils, 76.3 ohms each, insulated from one another

but wound together on the same former, protected from air currents and finally enclosed in a cork box, and by a sensitive mirror galvanometer of which the screen was placed in an adjoining room. Any slight final difference in the resistances of the two sides of the network is adjusted by bringing one of the galvanometer leads to a contact connexion on a

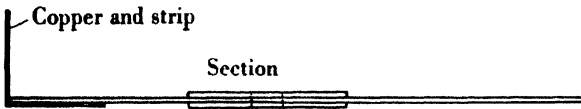
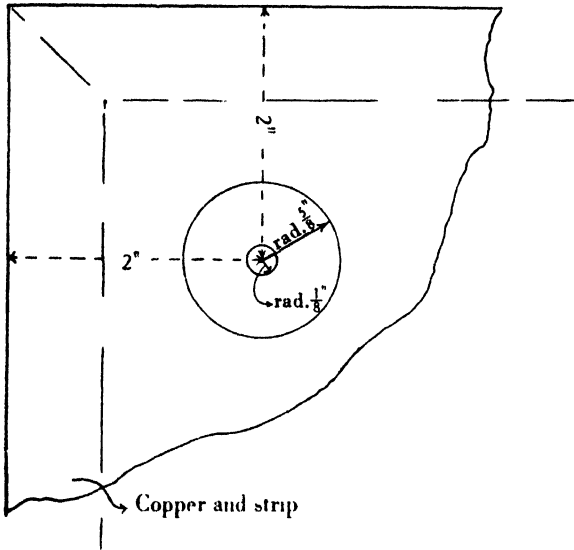
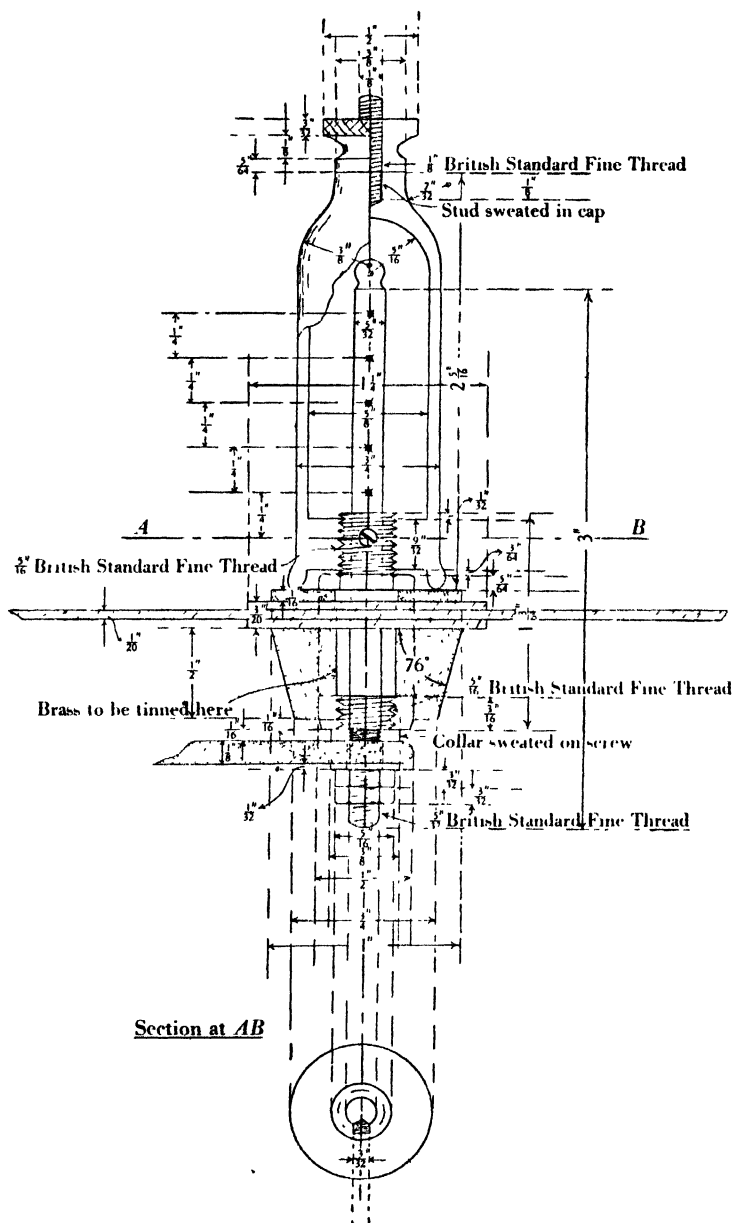


Fig. 5. Celluloid windows of poultry calorimeter covers (top corners).
Half full scale.

copper wire arranged in the same way as the slide wire on a Carey-Foster bridge.

The room in which the instruments are housed measures 15 ft. 8 in. \times 8 ft. 7 in. \times 7 ft. 8 in. and the walls and window are insulated with "cellotex" sheeting. Considerable difficulty was encountered in the regulation of the air temperature in this room to a sufficient degree of precision. How this was eventually achieved is described elsewhere (Deighton, 1936).



For the compensation of the heat generated by the bird an electrical heater, served by high capacity storage cells and itself of negligible heat capacity, is employed. It is made of constantan wire s.w.g. 28 of resistance 9.95 ohms suspended in the form of a zigzag network of spirals by strong linen thread wrapped round light steel bars on a base plate. The current is regulated by a variable rheostat with screw movement to the contacts which gives all required voltages at the terminals. The heat is computed from calibrated voltmeters across the heater terminal of the chamber and the current in the circuit as registered by a calibrated ammeter.

A similar heater is available for use in the animal chamber for testing the performance of the instrument.

The water vapour is varied in the compensation chamber in a very simple manner. A piece of muslin is spread over a horizontal support consisting of fine wires about a half an inch apart interwoven with a similar set of cross wires. This forms a net about 5×7 in. On two opposite sides the muslin dips in trenches filled with distilled water and the whole is covered by a sliding metal cover which is controlled by a spring and may be withdrawn to any extent desired by merely pulling a string passing to the outside. An airtight arrangement is made where the string passes to the exterior.

As an indicator of the variations in the water vapour content of the air in the chambers special multiple hair hygrometers are used but the final estimation in each experiment is made with a chemical hygrometer using pumice soaked in sulphuric acid as the absorbent, and prepared according to the recommendation of Haldane (1920). The aspirators are of rather more than 4 l. capacity.

Correction for water vapour differences. The residual water vapour differences affect the final result to such a small extent that it is merely waste of time to apply corrections for differences in temperature of collection, etc. This affords a welcome simplification but in spite of it the theory of the correction to be applied is confusing and must therefore be set out at some length.

Suppose that the final humidity of the air drawn from the animal chamber is h , and that of the air drawn from the compensation chamber is h_2 ; then assuming that the hair hygrometers register the *changes* in humidity reasonably correctly we have

$$\text{Original humidity of the animal chamber} = h_1 - \Delta h_1,$$

$$\text{Original humidity of the compensation chamber} = h_2 - \Delta h_2,$$

where Δh_1 and Δh_2 are the rises in humidity recorded in the respective chambers in the course of the experiment.

We thus have two possibilities in any particular experiment, either $h_1 - \Delta h_1 = h_2 - \Delta h_2$ or it does not. These require separate treatment.

In the first case the chambers start at equal humidities. Now let us suppose that the compensation chamber air gains in humidity in the course of the experiment at exactly the same rate as the air in the animal chamber. In this case there will be no correction to be applied since conditions have been exactly similar in both as to extent and time rate of rise. This, however, is rarely the case, so let us suppose that the relative humidity of the air in the compensation chamber is increasing by x per cent per minute more rapidly than that in the animal chamber. It is clear that in this case the heat required in the compensation chamber to balance the bridge will be too great, by the amount of heat required to vaporize the extra water which is being evaporated in this chamber.

This amount of extra heat is, however, not quite constant, even when the rate at which the humidity of the compensation chamber is gaining on that of the animal chamber is steady; owing to the fact that the humidity of the ventilating air has always to be raised as much above that of the ventilating air of the other chamber as the general humidity of the air of the compensation chamber is above that of the other at any particular moment.

Let v = the volume of one chamber in litres,

m = the mass of 1 l. of saturated aqueous vapour at $\theta^\circ \text{C.}$,

L_θ = the latent heat of vaporization of water at $\theta^\circ \text{C.}$,

and f = the air flow through the compensation chamber in litres/min.
 = air flow through animal chamber.

We have then:

Heat used in increasing the humidity of the compensation chamber air above that of the animal chamber

$$= \frac{vmx}{100} L_\theta \text{ cal./min.} \quad \dots\dots(\text{A})$$

Heat used in increasing the humidity of the air which *flows through* the compensation chamber to a point as much above that of the air flowing through the animal chamber as the humidity of the compensation chamber air is above that of the animal chamber air at the time when the air in question flows through

$$= \frac{fmx}{100} L_\theta t \text{ cal./min.,} \quad \dots\dots(\text{B})$$

where t is the time in minutes since the steady gain in humidity of the compensation chamber air began.¹

Suppose now that the chambers are not at equal humidities at the start (compensation chamber humidity higher say)—in this case even if $x=0$ more heat will be used in the compensation chamber to raise the air which flows through to the humidity of this chamber than will be used for a similar purpose in the animal chamber.

Let the initial difference in relative humidity be d per cent, then the extra heat used in the compensation chamber will be

$$\frac{fmd}{100} L_{\theta} \text{ cal./min.} \quad \dots\dots(C)$$

Hence the total correction to be applied to the heat required to be generated in the compensation chamber to balance the bridge is

$$-(A+B+C).$$

There is a small residual correction, empirically determined, depending on the small difference in heat capacity of the chambers, slight inequalities in the insulating properties of the air cells and of the base, non-linearity of variation of convection loss with temperature difference, etc.

Tests. The final tests of the instrument at constant heat input are shown in Table I.

There remains one possible source of error which is peculiar to the instrument owing to the transparency of its walls and which would not appear in the tests performed but which would affect determination made with a bird. This arises from the fact that the heat *radiated* from

¹ It appears at first sight as if the factor t here should be $\frac{1}{2}t$. It must be remembered, however, that it is a time rate with which we are dealing; thus we have, in steps, assuming a rise equal to the average of the minute to occur at the end of the minute:

$$\text{At the end of the 1st minute } B = \frac{fmx}{100} L_{\theta} \times \frac{1}{2},$$

$$\text{At the end of the 2nd minute } B = \frac{fmx}{100} L_{\theta} \times \frac{3}{2},$$

$$\text{At the end of the } t\text{th minute } B = \frac{fmx}{100} L_{\theta} \times \frac{2t-1}{2}.$$

As the time steps are reduced to (say) $\frac{1}{n}$ th of a minute we have at the end of the t th minute (nt th time interval)

$$B = \frac{fmx/n}{100} L_{\theta} \cdot \frac{2nt-1}{2} = \frac{fmx}{100} L_{\theta} \cdot \frac{2nt-1}{2n},$$

so that in the limit when n becomes infinite and the rise is steady

$$B = \frac{fmx}{100} L_{\theta} t \text{ as above.}$$

the hot wires of the heater in the compensation chamber is not of the same wave-length as that radiated by the feathers of a bird. To test this, a window, similar to the chamber walls, was constructed and the heater switched on at maximum heat at a distance of about 2 in. from the

Table I. *Final tests at constant heat input*

Date		Heat generated watts	Heat recorded watts	Error %
21 May	Morn.	9.57	9.47	-1.0
	Aft.	9.87	9.57	-3.0
22 "	Morn.	10.18	10.23	+0.5
	Aft.	10.18	10.29	+1.1
23 "	Morn.	10.08	10.11	+0.3
	Aft.	9.98	10.01	+0.3
24 "	Morn.	8.51	8.21	-3.5
	Aft.	8.23	8.12	-1.3
27 "	Morn.	8.17	8.19	+0.2
	Aft.	8.60	8.59	-0.1
28 "	Morn.	8.07	8.09	+0.2
	Aft.	8.42	8.67	+3.0
29 "	Morn.	6.58	6.66	+1.2
	Aft.	6.34	6.32	-0.3
30 "	Morn.	6.42	6.42	Nil
	Aft.	6.34	6.26	-1.3
31 "	Morn.	6.67	6.87	+3.0
	Aft.	6.58	6.70	+1.8
3 June	Aft.	5.54	5.51	-0.5
4 "	Morn.	5.45	5.43	-0.4
	Aft.	5.54	5.51	-0.5
5 "	Morn.	5.69	5.79	+1.7
	Aft.	5.62	5.76	+2.5
6 "	Morn.	5.69	5.86	+3.0
	Aft.	4.88	5.01	+2.7
7 "	Morn.	4.64	4.70	+1.3
	Aft.	4.91	5.02	+2.2
11 "	Morn.	5.06	4.91	-1.8
	Aft.	5.20	5.12	-1.5
13 "	Morn.	4.91	4.81	-2.0
	Aft.	3.61	3.60	-0.3
14 "	Morn.	3.61	3.36	-6.9
	Aft.	3.61	3.57	-1.1
17 "	Aft.	3.56	3.43	-3.6
18 "	Morn.	3.61	3.58	-0.8
	Aft.	3.55	3.51	-1.1

Standard deviation = $\pm 1.4\%$

or (rejecting observation 14 June Morn. by Chauvenet's criterion)

Standard deviation = $\pm 1.2\%$.

blackened bulb of a sensitive thermometer. No rise of the thermometer occurred for several minutes, after which a slow rise took place due to gradual heating of the celluloid. On removing the window a marked and sudden rise due to radiation to the bulb took place, showing that the celluloid is not appreciably transparent to the rays from the heater. Radiation from the bird's feathers will in any case be negligible since the

outer feathers cannot differ in temperature to any considerable extent from their surroundings.

Tests in which a bird was used to see how the instrument operated under these circumstances showed that the metabolism was liable to

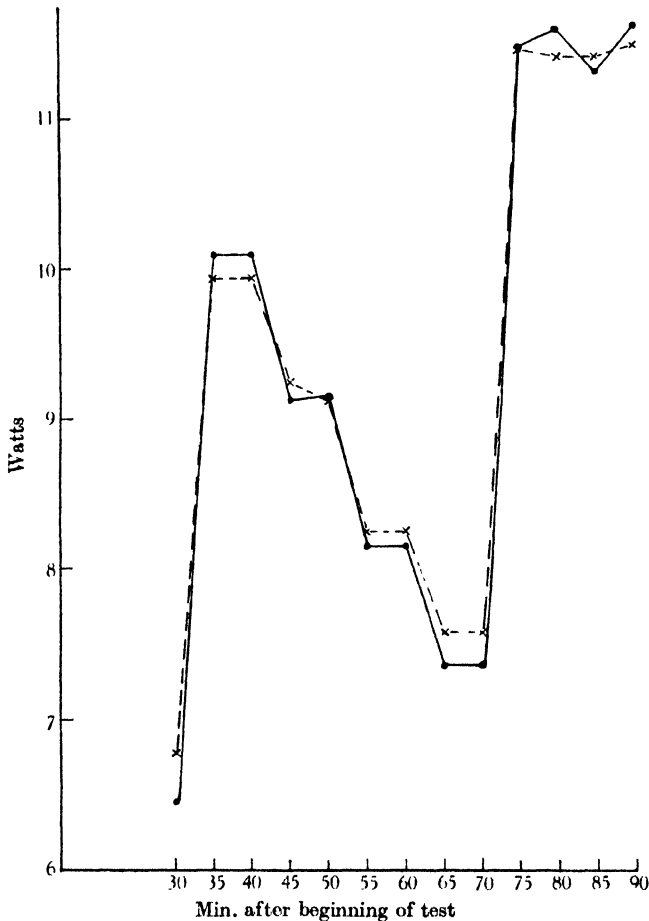


Fig. 7. Rapid variation of heat input.

Input —●— Registered —x—

vary very markedly during the course of an experiment especially with the different posture changes of the bird. It became necessary to put the calorimeter through a series of tests of quite exceptional severity not usually applied to such instruments, that is, the heat generated in the animal chamber had to be varied largely during the course of a test and

the accuracy with which the lag was taken up had to be noted. In the event the calorimeter acquitted itself quite surprisingly well, the error under these circumstances being hardly greater than under the usual conditions of test—a result which adds very materially to its value and to the trust which may be placed in the measurements made with it.

In Fig. 7 a typical graph is shown of the variations in the heat generated and the heat recorded in one such experiment and in Table II a summary of the results of further tests of the same kind is shown. The results as a whole make it clear that the course of a very variable metabolism can be followed with the instrument to a high degree of accuracy.

Table II. *Summary of results of tests with heat generation varied in the animal chamber*

Date 1935		Heat variation watts	Mean error %
Rise or fall in one step			
19 June	Aft.	8.21 up to 9.03	+ 5.4
20 "	Morn.	5.54 down to 4.84	- 2.9
	Aft.	6.36 up to 8.03	- 1.4
21 "	Morn.	4.25 " 4.85	- 2.9
	Aft.	9.27 down to 7.94	- 1.0
24 "	Morn.	10.36 " 8.64	+ 0.3
	Aft.	4.57 up to 6.12	- 0.8
25 "	Morn.	8.55 down to 6.44	- 0.6
	Aft.	5.06 " 3.74	- 3.2
Rise or fall in four equal steps			
26 June	Morn.	6.37 down to 4.88	+ 1.8
	Aft.	6.36 " 4.88	+ 2.0
9 July	Morn.	6.11 " 4.76	- 0.6
	Aft.	4.65 " 3.42	- 0.3
10 "	Morn.	4.75 up to 6.19	+ 0.3
	Aft.	9.60 down to 7.84	+ 1.1
11 "	Morn.	7.97 " 6.31	+ 1.1
Larger rise or fall in one step			
19 Aug.	Aft.	4.92 up to 8.28	Nil
20 "	Morn.	4.93 " 8.51	+ 1.4
21 "	Morn.	8.44 down to 4.66	- 1.7
	Aft.	8.46 " 4.69	+ 2.1

In a final test, adverse conditions of working were pushed to a point at which satisfactory working could not be expected, to get some idea of the performance of the calorimeter under such conditions. Arrangements were made so that the heat in the animal chamber could be varied at random by an observer seated in a room a short distance away. He was instructed to vary the heat as he thought fit both as to timing and amount up to a 250 per cent heat change and with the limitation that once a change had been made no further change should be made for 30 sec.

thereafter. Another observer at the instrument followed the changes as closely as conditions allowed. The result of this test is shown in Fig. 8, and although the individual observations are no longer very good individually, it is clear from the curves that the general performance is not unsatisfactory considering the conditions imposed. The integrated values of the two curves differ by less than 1 %.

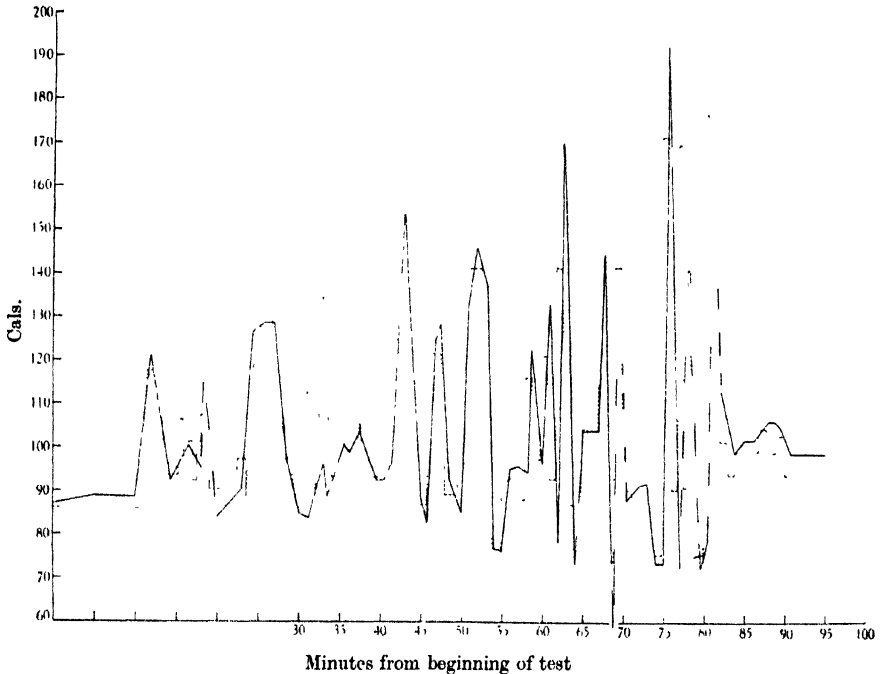


Fig. 8. Result of final test under limiting conditions.

— Heat generated in animal chamber. — Heat recorded.
 - - - Indicates trend of variation in recorded heat which was too rapid for actual measurement.

There remains the question of the behaviour of the calorimeter when a bird is placed inside the animal chamber. This is shown in Fig. 9, in which the observed movements of the bird are noted below the curve of metabolism. The metabolism computed for the resting position agrees well with the results of Nichita *et al.* (1933) who constrained their birds to this position by enclosing them in a cage too small to admit of their standing up or flapping their wings.

It is clear from the curve that the difference between the metabolism standing and sitting is considerable and that this must be taken into

full account in any energy investigations on fowls. Moreover, since the birds cannot live in the calorimeter, it is clear that it is advisable to have some record of their activity in the cages in which they are kept pending use in experiments.

A record showing automatically when, and for how long, the birds have been standing up and sitting down in their cages is obtained by focusing a parallel beam of light across the cage at such a level that the

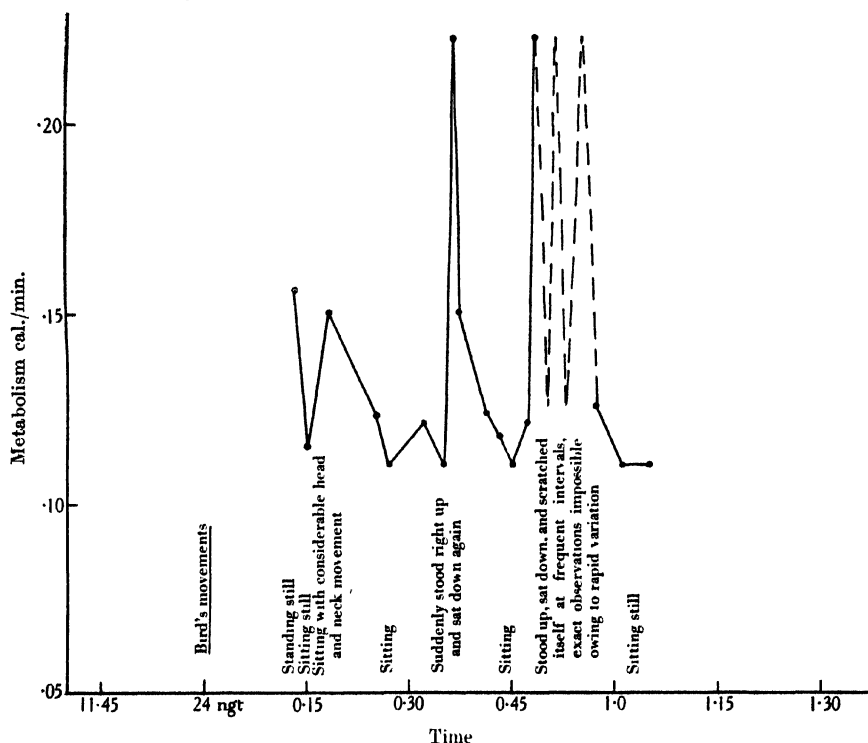


Fig. 9. Light Sussex fowl B, No. 140. Av. wt. 3099 g.

standing bird intercepts it while it passes above a sitting bird. This light beam is reflected several times across the cage by mirrors to form a network of light beams and finally falls on the sensitive element of a photoelectric cell. The photoelectric cell circuit is connected to a recording galvanometer which thus records when the bird stands up and obscures the light from the cell and when it sits down and allows the light to pass.

The effects of activity on the metabolism in fowls have been investigated at some length and the results of these experiments are at present in preparation for publication as paper II of the present series.

In conclusion I wish to express my thanks to Mr A. W. Mason who made the whole of the apparatus in the laboratory and later gave assistance in working the tests, as also to Messrs K. C. Williamson and G. A. Childs, the latter of whom was solely responsible for the inception and carrying out of the scheme for photoelectric registration of movement in the cages mentioned above. The final success achieved is in no small measure due to this keenness and perseverance which they brought to the work.

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FACTORS INFLUENCING THE PERCENTAGE OF NITROGEN IN THE BARLEY GRAIN OF HOOSFIELD

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1. INTRODUCTION

THIS investigation was undertaken in response to an enquiry whether winter rainfall had any influence on the percentage of nitrogen in the barley grain of Hoosfield, and whether this percentage showed any relationship with the yield of grain. The investigation was in no sense exhaustive, but in view of the clear-cut results obtained, a brief account of them may be of interest.

The data actually used consisted of nitrogen determinations on samples from the various plots of Hoosfield for the years 1893–1911 and 1914–28. In the year 1912 the whole field was fallowed, and subsequent to 1928 it was sown for several years with two varieties, and the rows were widely spaced in an attempt to check weed infestation. The values for 1913 and those subsequent to 1928 have therefore been excluded.

Plots 1–0 (no manure), 1–A (sulphate of ammonia), 4–0 (minerals), 4–A (minerals and sulphate of ammonia), and 7–2 (farmyard manure) were chosen for analysis. A general description of the experiment, with details of the manuring, has been published previously by Mackenzie (1924).

2. REGRESSIONS ON RAINFALL, SOWING DATE, AND YIELD

A preliminary investigation of possible rainfall effects was first undertaken. The rainfall for the three quarter-year periods, October–December, January–March and April–June, were calculated for each of the 34 years. The years were then divided into three approximately equal groups of high, medium and low rainfall independently for each of these quarterly periods, and the mean nitrogen percentage calculated for each group.

The results shown in Table I were obtained. It is clear that the effect of rainfall in the two winter quarters is small, but there is some indication of an effect of rainfall in the last quarter.

Table I. *Mean nitrogen percentage for low, medium and high rainfall groups*

Plot	1-0	1-A	4-0	4-A	7-2
(a) October–December rainfall					
Below 7.5 in.	1.44	1.64	1.43	1.55	1.84
7.5–10 in.	1.48	1.69	1.57	1.57	1.84
Above 10 in.	1.49	1.67	1.51	1.49	1.86
(b) January–March rainfall					
Below 5.5 in.	1.48	1.69	1.50	1.50	1.88
5.5–7.5 in.	1.49	1.65	1.52	1.57	1.86
Above 7.5 in.	1.44	1.65	1.50	1.56	1.79
(c) April–June rainfall					
Below 5.5 in.	1.57	1.83	1.64	1.67	1.87
5.5–7 in.	1.41	1.58	1.44	1.49	1.86
Above 7 in.	1.42	1.56	1.42	1.44	1.79

In order to assess this effect more accurately and also to investigate the relationship between yield and nitrogen percentage, the simultaneous partial regression of nitrogen percentage on April–June rainfall, sowing date and yield was calculated for each of the chosen plots.

So as to eliminate the major part of any slow changes occurring in the variables, the data were divided into the following sets of years, 1893–9, 1900–6, 1907–14 excluding 1912–13, 1915–21, 1922–8. All sums of squares and products were calculated from the deviations from the means of these sets. There are consequently 29 degrees of freedom associated with these sums.

The means, variances and correlations between the different variables are shown in Table II. The covariances are shown in the form of correlation coefficients, since the relationships existing between the different variables can then be more easily comprehended. Their conversion to covariances can, of course, be easily effected by means of the formula

$$\text{cov } xy = r_{xy} \sqrt{\{V(x) \cdot V(y)\}}.$$

Table II. *Variances and correlations (units as in Table III)*

Rainfall variance: 3.316. Sowing date variance: 228.4. Correlation: -0.3061 .

Plot	1-0	1-A	4-0	4-A	7-2
Variance of yield	5.151	9.676	9.402	18.841	28.815
Correlation with: Rainfall	-0.0846	$+0.0926$	$+0.0075$	$+0.0993$	$+0.1792$
Sowing date	$+0.0500$	-0.0354	$+0.0014$	-0.1999	-0.1266
Variance of nitrogen percentage	0.03031	0.04565	0.03614	0.03168	0.02216
Correlation with: Rainfall	-0.3859	-0.5011	-0.4143	-0.5314	-0.1562
Sowing date	$+0.5164$	$+0.3209$	$+0.4813$	$+0.5123$	$+0.4947$
Yield	-0.2864	-0.4665	-0.3990	-0.3832	-0.0820

The correlations of rainfall with sowing date, and of either with the

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yields, are all small. The nitrogen percentages show significant correlations with each of the other variables on most of the plots.

The partial regression coefficients obtained from these variances and covariances are shown in Table III, together with their standard errors, the residual standard deviations of a single determination, and the percentages of the variance accounted for by the regressions.

Table III. *Regressions of percentage nitrogen on April-June rainfall, sowing date and yield*

Mean rainfall: 6.01 in. Mean sowing date: 21 March.

Plot	Mean yield cwt.	Mean N %	Partial regressions of N % on					Residual s.e.	Variance accounted for %
			Rain in.	Sowing date days		Yield cwt			
1-0	5.0	1.474	-0.0265 ± 0.0149	+0.00517**	± 0.00179	-0.0255* ± 0.0114	0.138	37	
1-A	9.0	1.676	-0.0477* ± 0.0178	+0.00257	± 0.00214	-0.0290** ± 0.0100	0.166	40	
4-0	7.5	1.510	-0.0304 ± 0.0157	-0.00494**	± 0.00189	-0.0246** ± 0.0088	0.146	41	
4-A	17.0	1.544	-0.0393** ± 0.0144	+0.00394*	± 0.00176	-0.0113 ± 0.0058	0.134	43	
7-2	18.3	1.848	-0.0002 ± 0.0148	+0.00481*	± 0.00177	-0.0006 ± 0.0048	0.137	16	

* Significant at 5% level

** Significant at 1% level.

Apart from the plot receiving farmyard manure, the results are very consistent. On the plots receiving no organic manures an additional inch of rain produces an average decrease in nitrogen percentage of 0.0360, a delay of one day in sowing produces an increase of 0.00416, and an increase in yield of 1 cwt. per acre is associated with a decrease of 0.0226. Plot 1-A, which receives sulphate of ammonia only, has a somewhat higher mean nitrogen percentage than the other plots.

The effect of delay in sowing on the farmyard manure plot is very similar to that on the other plots, but this plot stands alone in showing no apparent effect of rain, and no association with yield. The farmyard manure plot has also a very much higher mean nitrogen percentage than the other plots.

The nitrogen percentage is decidedly lower in the inorganic plots at Rothamsted than on the corresponding plots at Woburn. On the farmyard manure plots the values are very similar.

As will be seen from the last column of Table III, the percentage of the total variance accounted for by the regression is of the order of 40 % for all plots except the farmyard manure plot.

In order to see whether the above differences in the regression coefficients were significant the standard errors of the differences between the coefficients of plot 7-2 and plot 4-A, and between plot 4-A and plot 1-A, were evaluated. It should be noted that in performing these tests of significance account must be taken of the correlations between

the yields and the nitrogen percentages of the various plots. The exact procedure is described elsewhere (Yates, 1939).

The results shown in Table IV were obtained. Since the difference in the regressions on yield for plots 4-A and 1-A is the largest of the differences between the inorganic plots, and itself does not quite reach significance, we may conclude that there is no evidence of any real differences between the inorganic plots. On the other hand, the differences between the farmyard manure plot and the inorganic plots for rainfall and yield may be taken as established.

Table IV. *Differences between the regression coefficients*

	7-2 - 4-A		4-A - 1-A	
Rainfall	+0.0391	± 0.0128	+0.0084	± 0.0151
Sowing date	+0.00090	± 0.00156	+0.00137	± 0.00184
Yield	+0.0107	± 0.0062	+0.0177	± 0.0095

Although the regressions of nitrogen percentage on yield are negative, they are not of such a magnitude as to indicate that the total nitrogen content of the grain is anywhere near constant. For this to occur the regression coefficients would have to be about ten times as large as the observed values. Thus the yield and the total nitrogen content are very highly correlated. This serves as a justification for studying the nitrogen percentage rather than the total nitrogen content. In general the fundamental relationships between the various factors which go to make up the end-product of a crop's growth are best comprehended if the variables actually studied are chosen so as to be as little correlated as possible.

Two further points should be borne in mind when interpreting the above regression coefficients. The first is that the regression on yield does not represent an effect, in the ordinary sense of the word, since both yield and nitrogen content are end-products of the same complex chain of causes. It represents, rather, an interrelation between these two end-products. The second point is that the regressions on rainfall and sowing date represent the residual effects of these factors after allowing for any direct effects on yield. Their total effects would be obtained by conducting the regression analysis on rainfall and sowing date only, omitting yield. The correlation of rainfall and sowing date with yield is actually exceedingly small, and the differences between the two sets of regression coefficients are consequently quite trivial.

3. COMPARISON WITH THE WOBURN RESULTS

The regressions on rainfall and sowing date are partial regressions. Owing to the negative (though not quite significant) correlation between rainfall and sowing date the total regression on each variate separately will be somewhat greater numerically than the corresponding partial regression. The actual values are shown in Table V.

Table V. *Total regressions on rainfall and sowing date*

Plot	Rainfall	Sowing date
1-0	- 0.0369	+ 0.00595
1-A	- 0.0588	+ 0.00454
4-0	- 0.0432	+ 0.00605
4-A	- 0.0520	+ 0.00604
7-2	- 0.0128	+ 0.00487

The regressions on rainfall in this table represent both the direct effect, and also the indirect effect due to the fact that the sowing date tends to be later in dry years.

These values may be compared with the similar values obtained from the continuous barley experiment at Woburn (Russell *et al.* 1936, pp. 187-90). The rainfall effect was studied in more detail than has been done here, the effect of an additional inch of rain falling at any given time from mid-February to the end of August being evaluated by the polynomial regression method. All plots were found to behave similarly, showing a decrease in percentage nitrogen with additional rain from mid-April to the end of July, which reached its maximum of -0.13 per inch of rain in the first week of June. The integrated value over the period April-June, which should be comparable with the values of Table V, was found to be -0.081. The rainfall effect at Woburn is thus nearly double that observed on the inorganic plots at Rothamsted. The Woburn results also indicate that a more detailed investigation of the rainfall effect at Rothamsted, and particularly the inclusion of July rainfall, may possibly account for some additional variance.

The regression on sowing date at Woburn (also a total regression, other variates being ignored) was +0.0067, which is very similar to the values of Table V.

4. VARIETAL DIFFERENCES AND OTHER LONG TERM CHANGES

The variety was changed somewhat frequently during the course of the experiment, as shown in Table VI. In order to see if there was any difference in nitrogen percentage between the different varieties the mean

nitrogen percentages were calculated for the periods of Table VI, and corrected for variation in rainfall, sowing date and yield by means of the regressions already given. Except for constant differences between plots, the values for all plots were found to be closely similar. The mean values for all five plots are therefore shown in Table VI.

Table VI. *Effect of variety on nitrogen percentage*

Period	Variety	Mean rainfall April– June (in.)	Mean sowing date days after 28 Feb.	Mean yield cwt.	Adjusted N %
1893–1897	Carter's Paris Prize	4.20	11.2	12.3	1.77
1898–1901	Archer's Stiff Straw	5.80	10.5	11.0	1.80
1902–1905	Hallett's Chevalier	6.98	5.2	13.5	1.71
1906–1910	Archer's Stiff Straw	6.86	24.0	14.8	1.55
1911, 1914, 1915, 1916	Archer's Stiff Straw	6.00	36.0	12.8	1.55
1917–1921	Plumage Archer	6.14	19.4	10.3	1.52
1922–1928	Plumage Archer*	6.16	32.7	8.4	1.48

* 1927 Spratt Archer.

A very marked reduction in nitrogen percentage in the later years is apparent. This reduction proceeds fairly steadily throughout the period of the experiment, and appears to have little association with variety. Archer's Stiff Straw, for example, gave a mean nitrogen percentage of 1.80 in the period 1898–1901, and only 1.55 in the period 1906–10. It is, however, probable that the changes in nitrogen percentage are really due to varietal modifications. Dr Hunter informs us that pure line Archer selections were introduced about 1908 onwards. These were higher yielding barleys with a lower nitrogen content than the original stock of Archer from which they were selected.

The Woburn plots did not show any consistent reduction of this nature: the two periods 1883–1906 and 1907–26 gave very similar values for those plots on which the manuring remained unchanged (*loc. cit.* p. 186). In the Woburn results, however, no correction has been made for changes in mean yield. Since the yields tended to be lower in the latter half of the experiment some increase in nitrogen percentage might be expected from this cause, and this might be sufficient to off-set reductions due to varietal improvement.

SUMMARY

The effect of rainfall, sowing date and yield on the percentage of nitrogen in the barley grain of certain representative plots on Hoosfield is studied.

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All these factors are shown to have marked effects. The farmyard manure plot differs from the others, both in mean percentage and in the effects of rainfall and yield.

Changes in variety appear to have had little apparent influence, but there is a progressive decrease in the percentage of nitrogen which cannot be accounted for by changes in any of the above factors, and which may well be due to varietal improvement.

Comparison is made with the results of the similar study on the permanent barley plots at Woburn.

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OVULATION AND THE DESCENT OF THE OVUM IN THE FALLOPIAN TUBE OF THE MARE AFTER TREATMENT WITH GONADOTROPHIC HORMONES

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(With Plate IV and One Text-figure)

INTRODUCTION

WHILE investigating the causes of sterility in mares it was found that abnormal conditions of the ovaries and irregularities of the oestrous cycle are the main factors concerned.

It does not appear to be the ovary itself which is primarily the cause of the trouble but rather that abnormal conditions of the ovaries and irregularities in the oestrous cycle are the results of an abnormal hormonal rhythm.

In order to get further information on the dose of gonadotrophic hormone necessary to induce oestrus and ovulation in the mare, and by so doing, be able to treat some of these cases, a number of abnormal mares and also ten normal pony mares have been treated at a field station. During the course of these experiments various observations on ovulation, and the passage of the ovum through the tube have been made and are reported here.

METHODS

The mares are tried daily with a teaser stallion to determine their oestrous periods and palpation of the ovaries per rectum is made as often as is necessary to follow the changes in the ovary.

For the normal mare in which the average length of the oestrous period is 6 days, a follicle matures in one of the ovaries, and just before ovulation, reaches a size of 4.5-6.5 cm. diameter in the thoroughbred and heavy breed mares, and 2.5-3.5 cm. in pony mares. This can be determined by palpation through the rectal wall in the same way that one can pick out coins of different denominations from the pocket.

Immediately after ovulation, the collapsed walls of the follicle can be palpated per rectum, and an indentation can be felt on the surface

of the ovary. In about 8 hr. the collapsed follicle fills with blood, and at this stage can be distinguished by the soft pulpy feeling of the fresh blood clot. In the next 24 hr. the corpus luteum gradually becomes firmer and harder and after 72 hr. can no longer be distinguished from the rest of the ovarian tissue, except that the ovary, with the corpus luteum, is larger than the other ovary.

Experience in palpating follicles per rectum before and after ovulation, and the subsequent development of the corpus luteum has made it possible to estimate the time of ovulation in mares fairly accurately.

RESULTS

The results of the treatment by injection of gonadotrophic hormones (pregnancy urine extract, and pregnant mare serum extract) in nine mares are given in Table I; seven of the mares ovulated after injection, and in one mare, on which a post-mortem was held, the ovum was found in the Fallopian tube (Pl. IV, fig. 1). Details are given in all these cases and an estimation of the number of hours between time of injection and ovulation is made.

In all cases the details and history of the mares are tabulated, the sizes of follicles are judged from previous experience in palpating follicles per rectum and measuring them post-mortem and any qualifying notes about these mares are made at the foot of the table.

Where follicles are shown as 3.5 and 2(3) this should be interpreted as one follicle measuring 3.5 cm. and 3 follicles measuring 2 cm.

For mares nos. 7 and 8 charts are given (Tables II and III) showing the oestrous cycles of the mares, the sizes of the follicles in the ovaries and the dose of gonadotrophic hormones given.

All the hormones used were commercial preparations except the dried anterior horse pituitary given to mare no. 7.

In mares nos. 1, 2, 3, 4 and 7, pregnancy urine extract is marketed as Physostab; and pregnant mare serum extract is Antostab.

In mares nos. 5, 6, 8 and 9, pregnancy urine extract is marketed as Antuitrin S.

Mare no. 7. This mare was destroyed on 30 November at 9 a.m., 138 hr. after injection, and 95 hr. after ovulation.

On post-mortem the fresh corpus luteum could be seen in the ovulation fossa of the right ovary (Pl. IV, fig. 2).

The Fallopian tube of the right ovary was carefully dissected so that the tube could be straightened out, and the straightened tube was cut

Table I

Date	Time in oestrous cycle when examined	Sizes of follicles in ovaries in cm.		Treatment	Result
		Rt. ovary	Lt. ovary		
		Mare 1. Percheron, aged 18. Had bred previously but barren for last four years			
14. ix. 38	Not in oestrus	3.5 and 2.0(3)	4.0(2)	3000 mouse units of pregnancy urine extract given intravenously	—
16. ix. 38	Not in oestrus	3.5 and 2.0(3)	—	—	Both follicles in left ovary had just ovulated and filled with fresh blood clot. Ovulation 40 hr. after injection
18. ix. 38	Not in oestrus	2.0	—	—	One follicle in right ovary had ovulated, and corpus luteum felt quite firm. Two of the 2.0 cm. follicles had disappeared and one remained. Ovulation about 60 hr. after injection
21. ix. 38	Mare was destroyed and post-mortem showed two corpora lutea in left ovary and one in right ovary, and also one 2 cm. follicle in right ovary.				
		Mare 2. Thoroughbred, aged 10 years. Had bred previously but barren for last three years			
24. ix. 38	Not in oestrus	4.5	—	—	—
3. x. 38	Not in oestrus	4.5	—	1500 mouse units of pregnant mare serum extract, and 400 units of pregnancy urine extract given intravenously	—
4. x. 38	Not in oestrus	4.5	—	—	—
5. x. 38	Not in oestrus	—	—	—	Follicle had ovulated in right ovary and corpus luteum felt quite hard. Ovulation occurred about 30 hr. after injection. No follicles have come up in either ovary from this time to 31. xii. 38 and mare has gone into anoestrus

Table I (continued)

Date	Time in oestrous cycle when examined	<div> <div>Sizes of follicles in ovaries in cm.</div> <div> <div>Rt. ovary</div> <div>Lt. ovary</div> </div> </div>		Treatment	Result
		Rt. ovary	Lt. ovary		
Mare 3. Thoroughbred, aged 15 years. Had bred previously but barren for last two years					
24. x. 38	1st day oestrus	3.0	—	2500 rat units of pregnancy urine extract given intravenously	—
25. x. 38	2nd day oestrus	3.0	—	—	Follicle in right ovary had ovulated and corpus luteum felt quite firm. Ovulation occurred about 30 hr. after injection. This mare did not come in oestrus again but went into anoestrus
26. x. 38	1st day dioestrus	—	—	—	
Mare 4. Thoroughbred, aged 12 years. Had bred previously but barren for last four years					
5. vii. 38	3rd day oestrus. Mare covered by stallion at 11 a.m.	5.5	—	100 rat units of pregnancy urine extract given intravenously at 4.30 p.m.	—
6. vii. 38	4th day oestrus, 3 p.m.	—	—	—	Follicle in right ovary had just ovulated and indentation on ovary could be felt. Ovulation about 22 hr. after injection
8. vii. 38	1st day dioestrus	—	—	—	—

N.B. This mare was examined later on and found to be pregnant.

At the beginning of the 1938 breeding season this mare had two large cysts in the right ovary; these were punctured and the mare came in oestrus 26 days later, a follicle came up in the right ovary to 5.0 cm. size, the mare remained in oestrus 8 days, did not ovulate and the follicle persisted. 28 days later this follicle was punctured and the mare came in oestrus 32 days later, and it was in this oestrous period that the above treatment was carried out.

Mare 5, Welsh pony, 11 years. Had bred previously but barren for one year (had not been mated)		
16. ix. 38	1st day oestrus	2.5 — 1000 rat units of pregnancy urine extract given intravenously —
17. ix. 38	2nd day oestrus	2.5 — — —
18. ix. 38	3rd day oestrus	— — — Follicle in right ovary had ovulated, and corpus luteum felt quite firm. Ovulation about 30 hr. after injection
19. ix. 38	1st day dioestrus	— — —
N.B. This mare had an oestrous period of 7 days from 4. viii. 38 to 10. viii. 38, and dioestrus from 11. viii. 38 to 15. ix. 38, so that the length of the oestrous period was reduced from 7 days to 3 days.		
Mare 6, New Forest Pony, aged 4 years. Bred a foal in June 1938		
4. ix. 38	1st day oestrus	2.5 — 1000 rat units of pregnancy urine extract given intravenously —
5. ix. 38	2nd day oestrus	3.0 — — —
7. ix. 38	3rd day oestrus	— — — Follicle in right ovary had ovulated, and corpus luteum felt quite firm. Ovulation about 30 hr. after injection
8. ix. 38	1st day dioestrus	— — —
N.B. This mare had an oestrous period of 9 days from 9. viii. 38 to 17. vin. 38 and dioestrus from 18. viii. 38 to 3. ix. 38; the length of the oestrous period was reduced from 9 days to 3 days.		
Mare 7, Thoroughbred, aged 22 years. Had bred previously but barren for last two years		
24. xi. 38	3rd day dioestrus, 3 p.m.	4.5 — 1000 mouse units of pregnancy urine extract given intravenously —
25. xi. 38	4th day dioestrus	4.5 — — —
26. xi. 38	5th day dioestrus, 10 a.m.	— — — Follicle in right ovary had just ovulated, an indentation could be felt on the ovary. Ovulation occurred about 48 hr. after infection
30. xi. 38	The mare was destroyed and on post-mortem a fresh corpus uteum was found in the right ovary (Pl. I. fig. 2).	

Table I (*continued*)

Date	Time in oestrous cycle when examined	Sizes of follicles in ovaries in cm.		Treatment	Result
		Rt. ovary	Lt. ovary		
13. ix. 38	1st day oestrus	1.5	—	Mare 8. Welsh pony, aged 8 years. Bred a foal in June 1938 2000 rat units of pregnancy urine extract given intravenously	—
19. ix. 38	7th day oestrus	3.5	—	—	Mare remained in oestrus 7 days, follicle matured to 3.5 size, but did not ovulate
24. ix. 38	5th day dioestrus	3.5	—	1000 rat units of pregnancy urine extract given intravenously	Follicle did not ovulate
N.B. The follicle in the right ovary gradually grew to 5.0 size by the eleventh day of dioestrus, and after this diminished in size and completely disappeared in the next oestrous period, when a follicle came up in the other ovary and ovulated. See Table III.					
31. viii. 38	2nd day oestrus	—	1.0	Mare 9. Welsh pony, aged 5 years. In foal 1938 and foetus washed out of uterus at approximately 105th day of pregnancy 500 rat units pregnancy urine extract given intravenously	—
6. ix. 38	8th day oestrus	—	2.5	—	—
8. ix. 38	10th day oestrus	—	—	—	Follicle had ovulated in left ovary, collapsed walls were filled with fresh blood clot. Ovulation 8 days after injection
9. ix. 38	1st day dioestrus	—	—	—	—

N.B. Previous oestrous period was 7 days from 9. viii. 38 to 15. viii. 38, dioestrus from 16. viii. 38 to 29. viii. 38, and the above oestrous period from 29. viii. 38 to 8. ix. 38. During this oestrous period the mare did not show to the teaser stallion on 2 and 3. ix. 38, although the follicle in the ovary was gradually increasing in size.

Table II. *Chart showing oestrous cycle of mare no. 7*

0 = Tried by teaser stallion and not in oestrus. x = Tried by teaser stallion and in oestrus.															R = Ovulation occurred.																	
	...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
October 1938	...																															
Oestrous cycle																							0		0		0		x	x	x	
Left ovary																																
Right ovary																																
Dates on which injected																																
hormones																																
November 1938	...																															
Oestrous cycle	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	x	x	x	x	x	x	0		0	0	0	0	0	0	0	0
Left ovary																																
Right ovary													3.5																			
Injected with hormones																	3.5					4.5	4.5	4.5	4.5	4.5	R					Mare destroyed

24 October. Subcutaneous injection of acetone dried anterior lobe of horse pituitary in fine emulsion in oil, 200 mg.

27 October. Subcutaneous injection of 1000 mouse units of extract of pregnancy urine (Physostab).

24 November. Intravenous injection of 1000 mouse units of extract of pregnancy urine (Physostab).

Table III. *Chart showing oestrous cycle of mare no. 8*

		0 = Tried by teaser stallion and not in oestrus. x = Tried by teaser stallion and in oestrus.										R = Ovulation occurred.																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
August 1938	...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
Oestrous cycle*		x	x	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	x	x	x	x	x	0	0	0	0	0	
Left ovary	
Right ovary	
September 1938	...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	30	
Oestrous cycle		0	0	0	0	0	0	0	0	0	0	0	0	x	x	x	x	x	x	x	0	0	0	0	0	0	0	0	0	0	0	0	
Left ovary	
Right ovary	
Date of injection	
October 1938	...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
Oestrous cycle		0	0	0	0	0	0	0	0	x	x	x	x	x	x	x	x	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Left ovary	
Right ovary		5-0	5-0	.	3-5	.	3-0	.	2-5	.	2-5	.	2-5	2-0	1-5	1-5
Days on which injected	
November 1938	...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	30	
Oestrous cycle		0	0	0	0	x	x	x	x	x	x	x	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Left ovary	
Right ovary	
Days on which injected	

13 September. 2000 rat units (Antuitrin S). Pregnancy urine extract given intravenously.
24 September. 1000 rat units (Antuitrin S). Pregnancy urine extract given intravenously.

* This oestrous period was 6 days, and occupied 28 July-3 August.

at position *A* in Text-fig. 1; an attempt was then made to recover the ovum in the following way. The first attempt was made by introducing a fine pipette into the uterine end of the tube marked *C*, holding the end marked *A* over a flat-bottomed watch glass. In spite of considerable pressure of saline, the fluid would not pass beyond the first inch of the tube. It was then cut at position *B*, and a second attempt to wash out the ovum was made by introducing the pipette at position *A*, holding

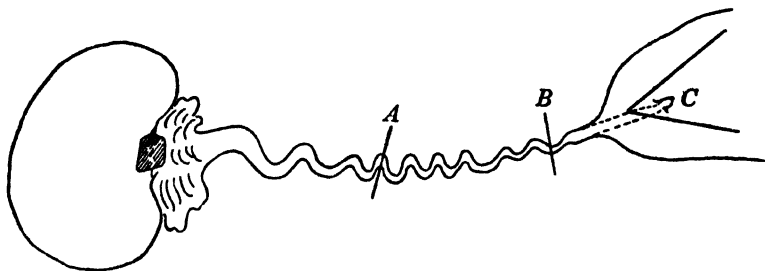


Fig. 1.

the end marked *B* over the watch glass. The fluid then passed down the tube and the ovum was recovered from the first few drops of saline which came through.

The total diameter of the ovum when measured with a micrometer after fixation in 5 % formalin was 113μ (Pl. IV, fig. 1).

As the ovum came out with the first few drops of fluid it would appear that the ovum reaches the uterine end of the Fallopian tube some 95 hr. after ovulation.

CONCLUSIONS

From a consideration of the details of the nine mares which have been injected with gonadotrophic hormones (see Table I) it would appear that independently of the time in the oestrous cycle, if a follicle is present in the ovaries and that follicle is sufficiently matured, the intravenous injection of 1000 to 3000 mouse or rat units of pregnancy urine extract (or in one case, 400 mouse units when given with 1500 mouse units of pregnant mare serum extract) will cause ovulation.

In those mares (nos. 3-6) which were in oestrus at the time of injection ovulation occurred from 22 to 30 hr. after injection; that this is an effect of the injection and not normal ovulation is shown by the fact that in the case of mares nos. 5 and 6 the length of oestrus was reduced from 7 and 9 days respectively to 3 days. In those mares which were not in

oestrus when injected (nos. 1, 2 and 7) but had moderately large follicles in their ovaries, ovulation occurred from 30 to 60 hr. after injection, without the appearance of oestrus by the mare.

In one mare (no. 8), in which ovulation did not occur although the mare was in oestrus when injected, and also in another mare (no. 9), in which the length of oestrus and the time of ovulation were not influenced by injection, it is thought that the follicles in the ovaries were not sufficiently matured at the time of injection for ovulation to take place.

The unusual behaviour of the follicle in the case of one mare (no. 8) is very difficult to explain, particularly as the second injection during dioestrus when the follicle had developed to a fairly large size did not have any effect.

Ovulation occurring 30-60 hr. after injection in the mares which were not in oestrus (nos. 1, 2 and 7) but had moderately large follicles in their ovaries, is comparable to the results of McKenzie & Terrill (1937) for the ewe, with ovulation 36-72 hr. after injection, and is similar to the findings of Cole (1936) in the rat, ewe, cow, and sow in which ovulation did not occur in less than 72 hr.

This ovulation occurring without the appearance of oestrus is similar to that which occurs in the ewe (Cole & Miller, 1933; Zawadowsky *et al.*, 1935*b*) but differs from conditions in the cow (Zawadowsky *et al.*, 1935*a*), where oestrus occurs after the injection of these hormones. There is no evidence that follicle growth was produced in any of the mares injected with these hormones.

SUMMARY

1. In mares which had a follicle of a sufficient size in the ovaries, in most cases the intravenous injection of 1000 mouse units or over of pregnancy urine extract caused ovulation at any time in the oestrous cycle.
2. In those mares which were in oestrus at the time of injection, ovulation occurred 22-30 hr. after injection, and the length of oestrus was reduced from 7 and 9 days to 3 days.
3. In those mares which were not in oestrus when injected ovulation occurred 30-60 hr. after injection without the appearance of any symptoms of oestrus.
4. Normal ovulation occurred after these injections, and in one case the ovum was recovered from the uterine end of the Fallopian tube about 95 hr. after ovulation, and 138 hr. after injection.



Fig. 1



Fig. 2.

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EXPLANATION OF PLATE IV

- Fig. 1. The unfertilized ovum of mare no. 7 recovered from the lower end of the Fallopian tube 138 hr. after injection with pregnancy urine extract and about 95 hr. after ovulation.
Fig. 2. Section through the ovaries of mare no. 7. 138 hr. after injection with 1000 mouse units of pregnancy urine extract. The fresh corpus luteum, dark in colour, is seen in the ovulation fossa of the right (lower) ovary.

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THE OESTROUS CYCLE OF THE MARE FOLLOWING REMOVAL OF THE FOETUS AT VARIOUS STAGES OF PREGNANCY

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INTRODUCTION

DURING an investigation on sterility in mares, it was decided to obtain a number of normal pony mares to try out the effect of gonadotrophic hormones on the induction of oestrus and ovulation. This decision was made at the end of the summer.

At this time great difficulty was encountered in procuring normal mares which were not pregnant. Because of this, it was decided to take mares in comparatively early stages of pregnancy and to remove the foetus. Details of the removal of the foetus from seven Welsh pony mares and the oestrous cycle following this operation are given below.

EXPERIMENTAL

The mares were originally chosen by palpating the pregnant uterus per rectum, and only taking those mares in which the foetus was comparatively small.

The foetus was expelled from the uterus in the following way.

The cervix was dilated by manual manipulation so that two fingers could easily be passed through.

It was then necessary in mares nos. 1-6 to separate the foetal membranes from the uterine mucosa, so that the end of a rubber tube could be introduced in the cervix without rupturing the foetal membranes.

The end of an equine stomach tube was then passed through the cervix and held in position with the right hand; an assistant connected the other end of the tube to the pump, and about 1-1½ gal. of warm saline was pumped into the uterus, to separate the foetal membranes from the mucous membrane of the uterus.

The tube was then taken out, and in mares nos. 1, 3, 4, 5 and 6 the head of the foetus was held with two fingers of the right hand through the cervix. The left hand was then introduced into the rectum and the

head of the foetus was pushed into the vagina by holding the foetus per rectum and pushing against the fundus of the vagina; by gently pulling on the head of the foetus, the whole foetus and membranes were pulled into the vagina.

In all these cases the foetus and amnion came through the cervix intact, but slight difficulty was met with separating the chorion in the tip of the pregnant horn. It came away in mares nos. 1, 3, 4 and 6 with gentle traction, but in mare no. 5 it broke away and a small piece of the foetal placenta was left in the tip of the pregnant horn.

In mare no. 2 the foetus, amnion and chorion were all expelled into the vagina after the uterus had been distended with saline, without any manipulation.

After dilation of the cervix in mare no. 7, the foetus was expelled in the vagina before the saline could be introduced, a matter of about 5 min.

Following the removal of the foetus from these seven mares, an ichthyol and gelatin pessary was introduced into the uterus.

The temperatures of the mares were taken daily for a week after this operation, but all mares made a spontaneous recovery without any rise in temperature. Mare no. 5 had a slight vaginal discharge for about a fortnight.

Five days after the removal of the foetus, the mares were tried daily with a vasectomized stallion to determine their oestrous periods.

Table I shows the ages of the mares, and the approximate ages of the foetuses which were removed. The age of the foetuses was estimated by taking crown rump and head length measurements, and comparing them with foetuses of known ages.

Table I

Mare no.	Age of mare years	Approximate age of foetus at time of removal days
1	5	98
2	5	63
3	4	98
4	5	105
5	4	91
6	6	86
7	2	51

Table II shows the oestrous cycle of the mares following this operation.

During the time the mares were being tried daily with a "teaser" stallion the ovaries were palpated per rectum about every 4 or 5 days

in dioestrus, and every other day in oestrus to determine if ovulation took place, and in Table II the approximate time of ovulation is given. It is possible to determine this by following the growth of the follicles in oestrus, and finding when the follicle has ruptured. In the pony mares used in this experiment, mature follicles ovulate when they are about 2·5–3·5 cm. diameter. This can be estimated by experience in palpating the ovaries and measuring follicles post-mortem, in the same way that it is possible to pick out coins of different denominations from the pocket. The time of ovulation given in Table II is only correct to the nearest day.

The mares were tried daily from August to December, by which time they had all gone into anoestrus, and none of them came into oestrus after the times given in Table II.

At the time of the removal of the foetuses in these mares, they were all in fairly good condition, but after the middle of October they gradually began to lose flesh at the same time as they were growing winter coats.

They were turned out night and day in paddocks, and when grazing was finished were given hay.

DISCUSSION

After parturition mares come in oestrus in 5–9 days. The average duration of oestrus is 6 days with variations from 3–65 days. Dioestrus varies from 6 to 83 days with an average of 17 days.

In the spring and autumn mares tend to have longer oestrous and dioestrous periods. This is because conditions are unfavourable for the ripening of follicles, and follicles are slow in reaching that rate of development which is necessary for the manifestation of oestrus, and are slow in maturing after the commencement of oestrus, giving a long oestrous period and a long dioestrous period.

In the seven mares reported here the onset of oestrus after removal of the foetus varied from 5 to 25 days in five mares and did not occur in two mares.

There does not appear to be any correlation between the stage of pregnancy at which the foetus was removed and the resulting oestrous cycle of the mare as Hammond (1938) found that oestrus occurred 4 days after the removal of the foetus at the 54th day of pregnancy in a Welsh pony mare.

This is of interest, as in the mare from about the 40th to 160th day of pregnancy, an active gonadotrophic substance appears in the blood

serum, reaching its maximum between 60 and 90 days (Cole & Hart, 1930). During this time, 40–160 days of pregnancy, it has been shown by Cole *et al.* (1931) that commencing at about the 40th day of pregnancy there is a gradual luteinization of follicles in the mares ovaries. In the earlier stages, luteinization had not taken place in all follicles and was only partial in some, but by approximately the 110th day complete luteinization of all follicles had occurred. In their work Cole & Hart gave crown rump measurements of foetuses and the condition of the mares ovaries, but our estimations of the stage of pregnancy have been made by comparing their foetal measurements with foetuses of known

Hammond (1938) found that luteinization of follicles had not occurred by the 84th day of pregnancy in one mare, but was complete by the 140th day in another, whereas the author found partial luteinization had occurred by the 58th day in one mare.

Before the gonadotrophic hormone appeared in the blood (40th day) no mares were treated.

Between this time and the time of maximum production of hormone (40–60 days) there were results from two mares, no. 7 (51 days) and Hammond's mare (54 days). The former did not come in oestrus while the latter did so in 4 days.

During the time of the maximum production of the hormone (60–90 days) there were the results from three mares no. 2 (63 days), no. 6 (86 days) and no. 5 (91 days). The first of these did not come in oestrus at all while the latter two came in oestrus at 6 and 5 days respectively.

Thus it appears that the presence or absence (as after normal parturition) of the gonadotrophic hormone in the blood does not affect in any way the maturation and ovulation of ovarian follicles a few days after the cessation of pregnancy.

In mare nos. 1, 3, 4 and perhaps 5, where there was the possibility that luteinization of all follicles had occurred, there was little if any effect on the time taken for the mares to come in oestrus, except possibly in the case of mares nos. 1 and 3 (98 days) which did not come in oestrus until 21 and 24 days respectively.

In the five mares which came in oestrus, the length of oestrus varied from 3 to 9 days. Ovulation occurred within 2 days of the end of oestrus in each case, although mare no. 5 did not ovulate in the first oestrous period, but ovulated in the second oestrous period after a short dioestrus of 6 days.

Ovulation took place in the first or second oestrous period of each

mare, but the subsequent cycles were rather irregular and although four mares came in oestrus again, they did not ovulate.

It is suggested that the time of year, namely autumn, at which these experiments were carried out was responsible for the irregularities of the cycle, particularly as all mares went into anoestrus in November.

SUMMARY

1. The removal of the foetus between the 51st and 105th day of pregnancy in the mare, did not have any detrimental effect in seven Welsh pony mares.

2. The subsequent oestrous cycles of the mares did not appear to be influenced by the stage of pregnancy at which the foetus was removed.

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THE IDENTIFICATION OF MINERALS IN SOIL COLLOIDS

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(With Five Text-figures)

INTRODUCTION

THE mineralogy of soil colloids¹ has in recent years received considerable attention, and much progress has been made in the separation and identification of minerals in this field. The search for the mineralogical composition is probably mainly due to the fact that a given soil colloid is not sufficiently characterized by its chemical composition alone. If it is considered that the minerals which form the bulk of most soil colloids so far investigated—kaolinite or halloysite, montmorillonite, beidellite and mica—all contain silica, alumina and water as main constituents besides varying amounts of iron, magnesium, titanium, calcium and the alkalies, it is readily understood that any given chemical analysis can be interpreted in many different ways as a mixture of two or more of these minerals. This state of affairs is further complicated by variations in the chemical composition of some of these minerals, which may be due to isomorphous replacements, by the occurrence of quartz and of oxides and hydroxides of iron and aluminium, and by the possible presence of amorphous material of unknown but variable composition. In view of all these difficulties, it is necessary to have methods for the direct determination of minerals apart from the possibility of estimating them from a chemical analysis.

In working with soil colloids it is possible to make a broad distinction between the methods used for the separation and the methods used for the identification of single constituents or minerals, although in a given case it is often very useful to use combinations of both methods, such as X-ray analysis before and after a Truog treatment.²

¹ The term "soil colloid" as used in this communication covers the entire clay fraction $<2\mu$ equivalent diameter but puts special emphasis on the smaller particles within this fraction. The subdivision of the clay fraction is discussed on p. 487.

² The term "Truog treatment" is used throughout this paper to denote the method evolved by Truog *et al.* (1937) for removing colloidal silica and free oxides and hydroxides of iron and aluminium from soils. The method consists in treating the sample with nascent hydrogen sulphide produced by adding alternately oxalic acid and ammonia to a suspension of the sample in sodium sulphide solution. The importance of this treatment in conjunction with X-ray diffraction analysis has been stressed by Alexander & Hendricks (1938).

The methods used for separation include various treatments for deflocculation or dispersion, destruction of organic matter, removal of certain constituents, grain size separations using the centrifuge or super-centrifuge, gravity separations using heavy liquids, flotation and partial flocculation methods. Of these methods only the Truog treatment will be discussed in this paper.

The methods used for identification, with which the present paper is mainly concerned, include X-ray, dehydration, optical and chemical analyses and their combinations. Methods using adsorption of dyes are not included, because the author has no practical experience of them, and it is difficult to judge on the published evidence (Correns (1925), Hardy (1931), Hüttig & Peter (1931)), how far they are specific for different minerals.

Before discussing these methods in detail it is necessary to point out one important difficulty, the variation of the properties of standard minerals with grain size. Soil colloids are not very well defined as to their grain size. In most cases it is possible only to state the equivalent radius derived from Stokes's law and to give an upper or an upper and a lower limit of grain size. The mineral identification is usually made by comparing the X-ray diagram, dehydration curve, refractive index and chemical composition of the soil colloid or a fraction of it with similar data for standard minerals, which are often composed of much larger particles. The extent to which the X-ray diagrams, dehydration curves and refractive indices of the standard minerals vary with grain size is generally not known with any accuracy, and this makes the identification doubtful for small divergencies between the properties of the soil colloid and the standard mineral. Far more data are needed on this question, especially if quantitative estimates of different minerals are to be made.

In spite of this difficulty it is in many cases possible to determine what minerals are present in a given soil colloid and to give a rough approximation as to their relative proportions. The methods in use in this laboratory and elsewhere will be shortly characterized in the order X-ray, optical, dehydration and chemical methods, and data will be given for a number of minerals known or believed to occur in soil colloids.

X-RAY METHODS

Of all the methods used for mineral identifications of soil colloids, the X-ray method is the most important one. It was first used by Hendricks & Fry (1930) and Kelley *et al.* (1931), and has later been used

by many other workers. It is now recognized that various silicates of the layer lattice type, the so-called clay minerals, form the main constituents of all soil colloids so far investigated. It is not intended to enter here into a description or discussion of the atomic arrangement of the clay minerals, but reference may be made to the summaries given by Bragg (1938), Kerr (1938), Lapparent (1937), and to the recent work of Hendricks (1938*a*).

The X-ray diffraction method gives the greatest amount of information if applied to single crystals of at least 0.2 mm. in one direction, and the least for crystal powders without any preferential crystallographic orientation of the single crystals within the powder. A powder with some degree of orientation, i.e. an "ordered aggregate", takes an intermediate position, giving a so-called fibre diagram. As single crystals of soil colloids are not large enough to be used in X-ray work, only the powder method and the method of ordered aggregates remain. Powder diagrams of various clay minerals are very similar to each other, and in mixtures many lines may coincide. The method of ordered aggregates is especially important for the following reason. The crystal structures of most clay minerals can be considered as being built up from sheets of various ions, where the composition and arrangement of the sheets are all very similar, and the main distinguishing feature is the number of sheets piled on top of each other. This number of sheets corresponds to a characteristic of the crystal lattice, which is known as the basal spacing. On the X-ray diagram of an ordered aggregate the basal spacings can be seen with greater certainty and measured with greater accuracy than on an ordinary powder diagram, where it is often not possible to decide whether a given diffraction line corresponds to a basal spacing or not. The value of the aggregate method as an addition to powder diagrams is, therefore, very great indeed.

The powder method has been described so often that it seems sufficient to refer to the literature. An excellent summary has recently been given by Möller (1937), and Favejee (1939) has described its application to soil colloids with a special camera in which the air is replaced by hydrogen. Care should be taken to keep all conditions strictly standardized. Filtered iron and cobalt radiations are mainly used in our own work, but chromium and copper radiations have also been used by other workers. As most soil colloids contain appreciable amounts of iron, which absorbs copper radiation and causes uniform blackening of the photographic film, copper radiation seems unsatisfactory.

Ordered aggregates can be made in several ways. Grim (1934) has

described a method of slow sedimentation, in which a microscope slide (or a glass rod) is immersed in a clay suspension, and time is allowed for a sufficiently thick layer to form. Aggregates can also be made quickly by centrifuging a clay suspension against a flat surface, such as a cover glass or piece of cellophane supported by a rubber bung in a centrifuge tube, or by sucking the suspension through a membrane filter and letting the filter cake dry after it has been carefully peeled off the filter. A slow method, which gives aggregates of a high degree of orientation, is to allow a concentrated clay suspension to evaporate completely. It is sometimes useful to let the soil suspension settle on a thin mica flake, and to use the sharp basal mica reflexions as calibration marks. The ordered aggregates can be deposited on either flat or curved surfaces and X-ray diagrams can be taken in cylindrical or plate cameras. For the aggregate method we have used an X-ray spectrometer with a variable distance between plate and crystal holder, and for the powder method a camera of 58 mm. diameter.

From the X-ray powder diagrams a number of reflexions are obtained which are characterized by their position, width and relative intensities, and which can be expressed as lattice spacings; from the aggregate diagrams a series of similar reflexions is obtained, which correspond to basal spacings. Some or all of the latter may be found on the powder diagrams. The lattice spacings are given in Å units ($1\text{Å} = 10^{-8}\text{ cm.}$) and the intensity is estimated in five steps, viz. very strong, strong, medium, weak, very weak. The range of lattice spacings in soil diagrams varies from 1 to at least 20 Å, and the X-ray equipment should be such that the larger spacings can be measured accurately.

The interpretation of these data is sometimes difficult. If a mineral is present in fairly large amounts, all its diffraction lines as observed on a standard material should be present in their correct positions and relative intensities. Diagrams of most standard minerals can be found in the literature, but both the positions and intensities of the diffraction lines may be changed to some extent by isomorphous substitutions, and the intensities also by orientation and absorption, especially if iron or chromium radiations are used. These effects have been discussed in detail by Gruner (1933) and by the writer (1934).

For mixtures the complete diagram of each component should be present with the diffraction lines in the same relative intensities and in the same positions as in the standard mineral diagrams. If a mineral is present in small amounts, it may be that all medium and strong lines can be found but not the weak lines, or that only the strong and very

strong lines occur. If lines overlap, the relative intensities will still give valuable clues. We have found in our own work that all soil-clay fractions, which had not been subdivided into different grain-size groups, were mixtures of several minerals. A graphical method of interpretation has been found very useful in such cases. X-ray diagrams are plotted with lattice spacings as abscissae on a logarithmic scale, and with the intensity in five equal steps as the ordinate. The use of the lattice spacing instead of the diffraction angle has the advantage that diagrams taken with different wave-lengths can be compared with each other.

The quantitative estimation of mixtures from X-ray powder photographs can be based on absolute intensities or on a comparison with standard mixtures. There are great difficulties inherent in both methods, even for metals and simple salts. Full discussions are found in recent summaries by Brentano (1938), Brindley & Spiers (1938) and Schäfer (1938), and applications for the quantitative determination of quartz are given by Nahmias (1932, 1933) and by Clark & Reynolds (1935). In the opinion of the writer a very great deal of preliminary work will be required before quantitative estimates for the clay minerals present in soil colloids can be given from X-ray data alone, and it may be that the difficulties will prove insurmountable. It is, however, quite feasible to give rough estimates of the order of $\pm 20\%$, and further information can be obtained by a combination of X-ray analysis with other methods.

OPTICAL METHODS

Optical determinations on soil colloids can be made either while the colloid is in suspension or on the air-dry or oven-dry material. In suspension the double refraction due to electrical, magnetic or mechanical orientation can be determined, and the refractive index can be measured by the immersion method with an ultramicroscope or with dark field illumination.

Measurements of this kind, using double refraction after orientation in an electric field, have been made by Marshall (1930, 1935*a*). The double refraction was found to vary with the voltage applied, with the cation used and to a small degree with the concentration. In most cases there was no saturation value with increase in voltage, and it seems, therefore, that more data are needed before this method can be used for mineral determinations. No other work on soil colloids using this method appears to have been published. Measurements of sign and amount of double refraction after mechanical orientation have been made for

bentonite suspensions by Buzagh (1929) and others, but do not seem to have been made for soil colloids.

Refractive index determinations on colloid suspensions under dark-ground illuminations have also been described by Marshall (1935*a*). The liquid used, potassium mercuric iodide, probably caused coagulation and base exchange reactions, and few standard minerals seem to have been investigated by this method.

Although optical measurements on soil suspensions are not difficult to make, it seems that it is not possible at present to base mineral identifications on such measurements, especially as neither the variation in the properties of standard minerals nor the behaviour of mixtures of standard minerals is known.

The optical investigation of soil colloids after drying is far more commonly used. The refractive index or range of indices is measured by the immersion method, and the interference figures of aggregates are observed. The double refraction may be inferred from such measurements, or can be observed directly if the thickness of the specimen is known with accuracy.

The refractive indices of some clay minerals vary with their water content and with the immersion liquid, as has been shown by Correns & Mehmel (1936) and by van Baren (1936), and through isomorphous replacements. All these variations are large for montmorillonite and small for mica. The way in which the refractive index varies with grain size is, again, in most cases unknown. Another serious difficulty is caused by coatings of iron oxides or hydroxides, which are often found on larger soil grains and probably also coat the colloid particles. It is found in our own work that a Truog treatment often reduces the refractive index considerably (from 1.60 to 1.56 in one case). This is probably due to the removal of coatings which are richer in iron than the interior. The range of refractive indices encountered in soil colloids is roughly from 1.48 to 1.62, and the range of refractive indices for the montmorillonite group alone is of the same order (1.50-1.61). It seems to follow that refractive index determinations alone are of doubtful value, and several cases are known where mineral determinations based only on such data were later disproved by X-ray analysis. In combination with X-ray work, however, they may prove useful by giving clues to the chemical composition or water content and also by giving corroborative evidence.

The optical interference figure of aggregates of soil colloids is sometimes surprisingly good, except when the colloid is rich in organic matter and iron oxide. It is very often biaxial negative and, according to the

data of Hendricks & Fry (1930), the angle $2V$ varies from 0° to 40° . The diagnostic values of both the interference figure and the double refraction are limited. It may perhaps be stated generally that colloids containing minerals of the montmorillonite or mica type have a higher double refraction than colloids containing minerals of the kaolinite type, but it does not seem to the author that more detailed statements would be justified at present.

DEHYDRATION METHODS

In dehydration work three types of methods can be distinguished, viz.

- (1) Vapour pressure—water-content determinations.
- (2) Dehydration curves.
- (3) Heating curves.

(1) The first method has been used extensively by many workers, Thomas (1928), Puri *et al.* (1925), Kuron (1930, 1936), Alexander & Haring (1936) and others. It seems likely that the exchangeable ions are of greater importance than the minerals present in the soil colloid, but it is possible that the method could be used for mineral determinations, if sufficient preliminary data were given. At present such data are not available.

(2) *Dehydration curves.* The loss in weight of a soil colloid upon heating to higher and higher temperatures is recorded and plotted against the temperature. The resulting curve is then compared with the curve obtained from standard minerals. There are several variations of this method.

(a) *Intermittent heating.* The sample is heated to a given temperature, and weighed from time to time until no further loss in weight is observed; it is then heated to a higher temperature until no further loss occurs, and so on. The samples are cold while they are weighed. This is the method used by Ross & Kerr (1930), Kelley *et al.* (1936) and many other workers; it is also used in this laboratory.

(b) *Continuous heating.* The sample is heated at a constant rate which may vary between 2 and 200 hr. for a rise in temperature from 20 to 1000° C. and the loss in weight is recorded, that is to say, the samples are weighed hot. This is the method described by Longchambon (1936).

(c) *Single heating.* A number of samples equal to the number of different temperatures is used, and each sample is heated for the same length of time to a different temperature, for instance with 50° intervals. This method has been used by Dunstall (1938) for chlorites.

Intermittent heating has been most widely used. Continuous heating requires either automatic or very frequent weighings, and single heating requires more material than the other methods. It is possible that the dehydration curves, according to single and continuous heating methods, show more detail, and the latter is perhaps the best, as it uses very little material, is comparatively quick and the apparatus can also be adapted to rehydration studies. In all three methods the actual humidity of the air in contact with the sample should be kept constant, as variations will affect the curves.

It is generally assumed that the loss in weight of one mineral upon heating is not affected by the presence of a second mineral, and the dehydration curve of a mixture is considered as the superposition of curves due to different minerals. As far as the writer is aware, no dehydration curves of mixtures of known minerals have been published, and the validity of the above assumption is, therefore, not proved. There are some further difficulties in the dehydration method. The loss in weight which is measured is not necessarily due to a loss of water, but may be due to the loss of CO_2 from carbonates or organic matter or to the loss of some other volatile constituent of the soil colloid. Carbon determinations by combustion on a number of colloids, which had been prepared in this and other laboratories after the conventional removal of organic matter by hydrogen peroxide or potassium hypobromite, invariably showed carbon to the amount of 1 or 2% and even occasionally up to 6%. Similar observations have been published by Puri & Sarup (1937). The oxidation of divalent iron or manganese would reduce the apparent water loss. A further difficulty is the degree to which the dehydration curve of a mineral is affected by its grain size. The work of Longchambon (1936) and of Kelley *et al.* (1936) shows this effect for muscovite, dickite and pyrophyllite, but our own unpublished work on montmorillonite fractions, produced by supercentrifuging, showed no differences in dehydration curves of three fractions within the range of $0.8\text{--}0.04\mu$ equivalent diameter.

Dehydration curves of many minerals have been obtained by one or other of the methods described, but the results have not been collected in a systematic way, and no data for the different methods on the same materials are available. It can perhaps be stated generally that, using the method of intermittent heating, water from organic matter, iron and aluminium hydroxide and the reversibly held or "adsorbed" water of the clay minerals are lost below 400°C ., lattice hydroxyl from clay minerals between 400° and 600°C ., and some water from mica, probably also present

as hydroxyl, at still higher temperatures. Very large losses of water below 400° C. may, therefore, be due to the presence of a mineral of the montmorillonite group, and very large losses between 400° and 600° C. to the presence of halloysite or kaolinite. The evaluation of dehydration curves of soil colloids without X-ray and chemical data seems of uncertain value but, in conjunction with the other methods, dehydration curves are of great diagnostic interest.

(3) Heating curves are used instead of, or in combination with dehydration curves. The specimen is heated in an oven side by side with aluminium powder or some other inert material, and the difference in temperature of the two samples is plotted against the oven temperature. In this way a curve results which may show endothermic or exothermic humps. With clay minerals endothermic effects are due to the release of adsorbed water and to the breakdown of the lattice, and exothermic effects may be due to the oxidation of divalent iron or to the formation of new silicates at higher temperatures. Different clay minerals show characteristic heating curves, and it is claimed that the method is applicable to mixtures. The method has been used extensively in France, and curves for a number of standard minerals are available (Orcel, 1926, 1933). The variation of the curve with varying grain size of the minerals is only known in very few cases, for instance for the magnesian mineral sepiolite (Migeon, 1936). The method has been applied to soils by Agafonoff (1936), and it seems from his curves that the position of the humps is clearly affected by the presence of other minerals. A sample of kaolinite showed a large endothermic effect at about 570° C., and a soil claimed to contain kaolinite showed the effect at 650° C. The position of the hump depends on the rate of heating, and it is to be expected that dilution will shift it to a higher temperature, but in the opinion of the writer much standardizing work will have to be done before the method can be used with confidence for mineral identification.

CHEMICAL METHODS

The ordinary methods of silicate analysis, which give the chemical composition of a soil colloid, need no discussion here, but attention may be directed to the findings of E. S. Larsen (1938) with regard to the accuracy of high-class silicate analysis. The common practice of determining only ignition loss, silica, alumina, iron oxide and titanium oxide in order to obtain iron-alumina and silica-sesquioxide ratios is, in the opinion of the writer, unsatisfactory. Magnesium and divalent iron are

able to replace aluminium in six-coordination in many silicate layer lattice minerals and their proportions should be known. The alkalis may be present in some form of mica, which is a very common constituent of soil colloids, and should therefore also be known.

The difficulties in interpreting chemical data without any knowledge of the mineralogical composition have been pointed out in the introduction; in conjunction with X-ray, dehydration and optical data it is often quite possible to account for the bulk of the analysis in a fairly satisfactory way.

It is not intended to review here all the chemical methods which have been used for separating various minerals, beginning with the "rational clay analysis" and ending with the action of various organic oxyacids at constant or varying pH. There is no method known at present that will completely dissolve one mineral without attacking several other minerals in some degree. Again, data for standard minerals of varying grain size are rare, although obviously in all these methods the grain size is of paramount importance. The data of Thiébaud (1925) for the action of hydrochloric acid, sulphuric acid and sodium hydroxide on clay minerals apply only to fractions above or below 2μ and not to still finer grain sizes. The borofluoric, Line & Aradine (1937), and borosilicic acid, Knopf (1933), methods for the separation of quartz from other silicates, which work fairly well on larger grains, cannot be applied to mixtures below 2μ equivalent diameter.¹

Combinations of chemical and X-ray methods may, however, be useful. Alexander & Hendricks (1938) have used X-ray analysis before and after a Truog treatment, and report that the Truog treatment is very effective for removing goethite, α -FeOOH, but that it seems to attack the aluminium silicates to some extent, if the iron hydroxide is to be completely removed. Both these observations are confirmed in our own experience, but it must be admitted that the experimental directions, Truog *et al.* (1937, pp. 109–11), are given for the whole soil material, and have been applied by us to the colloid fractions without modification. Some experimental data on this question will be given later.

Another combination of methods is X-ray analysis before and after heating to certain temperatures. This method has been used by Noll (1936) for the determination of small amounts of montmorillonite in the presence of large amounts of kaolinite, and Kelley & Dore (1938) have applied the same method to soil colloids. It can perhaps be further improved by a treatment with dilute acid and alkali after the heating in

¹ The writer is indebted to Dr E. J. King for this information from unpublished work.

order to remove and determine the breakdown products (metakaolinite), which cause diffuse scattering in the X-ray analysis.

Reliable mineralogical determinations on soil colloids are so rare that it is impossible as yet to give any correlation with climate, parent material or soil group. The difficulties and limitations of the identification methods developed so far have been stressed deliberately, because some published mineral determinations seem to be based on insufficient data and may, therefore, not be correct. Such incorrect determinations would not only make it very difficult to find correlations, but might also discredit the mineralogical methods.

One result, however, seems to be fairly general; it is reported by several authors and is nearly always found in our own work. Whenever the clay fraction of a soil is subdivided into different grain-size groups, these groups show differences in their mineralogical composition. The differences are due not only to the commonly observed decrease of quartz with decreasing grain size, but also to the presence and relative proportions of various clay minerals. In view of this fact it seems advisable to subdivide the clay fraction into at least two and preferably into three or more fractions, especially if details are desired about the mechanism of weathering of different minerals. International agreement about the range of these fractions seems desirable. The simplest course would be to continue the Atterberg scale to 0.2μ and 0.02μ equivalent diameter.

AMORPHOUS MATERIAL

The methods outlined above are concerned with the identification of minerals in soil colloids, and the X-ray method in particular has only been discussed in its application to crystalline material. In the past the view had been widely held that the soil colloids were mainly composed of amorphous mixed gels. After the introduction of X-ray methods, it has often been assumed that soil colloids were crystalline throughout. It is now possible to define amorphous mixed gels as material of variable chemical composition with a fair percentage of water, a smooth dehydration curve of the adsorption type and an X-ray diagram with one or two wide haloes but no sharp diffraction lines. The haloes correspond to the average distance of atoms or groups of atoms within the gel. The mineral allophane described by Ross & Kerr (1934) represents such a material. It is impossible to say at present whether or to what extent such amorphous gels exist in soil colloids. Some indication of their presence has been given in the work of Roborgh & Kolkmeijer (1936), but the data

do not give conclusive evidence. A quantitative X-ray study comparing line and background intensity after the addition of some standard crystal powder and using monochromatized radiations from several wave-lengths, would probably settle this point for any given material, but no such work seems to have been published. It must also be remembered that the transition from crystallized to amorphous material is probably gradual, but again no accurate data on the width of diffraction lines from soil colloids are available. Such measurements would be complicated by the fact that the diffraction lines may be widened, not only by the small size of the diffracting units, but also by lattice irregularities arising from isomorphous replacements or mechanical disturbances.

STANDARD DATA FOR MINERALS OCCURRING IN SOIL COLLOIDS

Many of the minerals which are known or believed to occur in soil colloids have been studied extensively, and where detailed optical, chemical, dehydration or X-ray data have been published, it will be sufficient to give a selection of references which will provide sufficient information for comparisons with soil colloid data. X-ray diagrams in the graphical form described on p. 481 are given in Figs. 1, 2, 3 and 5, and are based on our own data, unless otherwise stated. The values given for refractive indices refer to sodium light, and show in many cases the variability with minor changes in the chemical composition of the minerals. The double refraction, therefore, cannot be taken as the difference of the extreme values quoted.

Quartz and cristobalite

Quartz has the composition SiO_2 and the refractive indices $n_\omega = 1.544$, $n_e = 1.553$. X-ray powder data are given in Fig. 1, *a*, *b*. Quartz is not a layer lattice mineral and there are, therefore, no basal spacing lines. The strongest quartz diffraction line at $d = 3.35$ Å nearly coincides with a strong mica line at $d = 3.34$ Å, and in the presence of mica the identification of quartz by X-rays should be based on the occurrence of the lines at $d = 4.32$, 1.830 , 1.552 and 1.384 Å, which are the strongest lines for quartz smaller than 0.2μ equivalent diameter. Quartz has a much better diffracting power for X-rays than the other minerals in clays, and in a mixture with 30% quartz the quartz lines are usually by far the strongest lines, especially at higher angles of diffraction. The detection of small quantities of quartz in a mixture is, therefore, comparatively easy.

Quantitative determinations of quartz in mixture with kaolinite and other minerals have been made by Nahmias (1932, 1933) and by Clark & Reynolds (1935).

We have found quartz in varying proportions in nearly all soil clay fractions $< 2\mu$, which had not been further subdivided into different grain-size groups. The amount present usually decreased rapidly with decreasing grain size. It was never found in the finest supercentrifuged fractions, corresponding to Grim's "superfine" clay, and only rarely in the next coarser fraction. Similar results have been reported by Bray *et al.* (1935) and others.

The high temperature modification of cristobalite, chemical composition SiO_2 , refractive index $n=1.486$, seems a possible product of crystallization of amorphous silica at low temperatures, and has been found in several opal and flint samples by Levin & Ott (1934), who identified it by means of its X-ray powder diagram. The refractive indices of their samples varied between $n=1.41$ and 1.43 . The occurrence of cristobalite in a soil colloid has been mentioned by Jacob, Hofmann & Loofmann (1935), but no experimental details are given. The X-ray data, Fig. 1, c, are due to R. G. W. Wyckoff (1922).

The refractive indices of amorphous silica and alumina at various stages of hydration and in the absence and presence of salts have been measured by Hellmers & Köhler (1933, 1934).

Oxides and hydroxides of aluminium

The following crystallized compounds are known:

		Refractive indices
1. $\alpha\text{-Al}_2\text{O}_3$	Corundum	1.760-1.769
2. $\gamma\text{-Al}_2\text{O}_3$	γ -Corundum	1.650-1.690
3. $\alpha\text{-AlOOH}$	Diaspore	1.702-1.750
4. $\gamma\text{-AlOOH}$	Boehmite	1.630-1.640
5. $\gamma\text{-Al(OH)}_3$	Hydrargillite or gibbsite	1.554-1.576
6. $\gamma'\text{-Al(OH)}_3$	Bayerite, unstable	1.55

Fricke & Severin (1932) and Hüttig & Wittgenstein (1928) have studied the dehydration of the different types of hydroxides of aluminium, and Achenbach (1931) has given additional dehydration, optical and X-ray data. The X-ray diagram of γ -corundum has been measured by Hansen & Brownmiller (1928) and Weiser & Milligan (1932). X-ray data for bayerite are given by Fricke (1929) and Lehl (1936), for corundum by Harrington (1927), for diaspore by de Jong (1930) and for all of the above minerals by Boldyrev (1938). X-ray diagrams are also reproduced in a paper by Böhm (1925). Our own data are shown in Fig. 1, d, e, f.

All these compounds, except γ -corundum and bayerite, are known as minerals, and seem to be possible components of soil colloids, especially in the case of tropical soils which are low in silica. Sedletzki (1938) failed by the X-ray diffraction method to find any of these minerals in a number of soil colloids, including those from red earths. Hendricks & Fry (1930) reported the presence in two soil colloids of bauxite (presumably boehmite), characterized by its X-ray diagram. Vageler (1938)

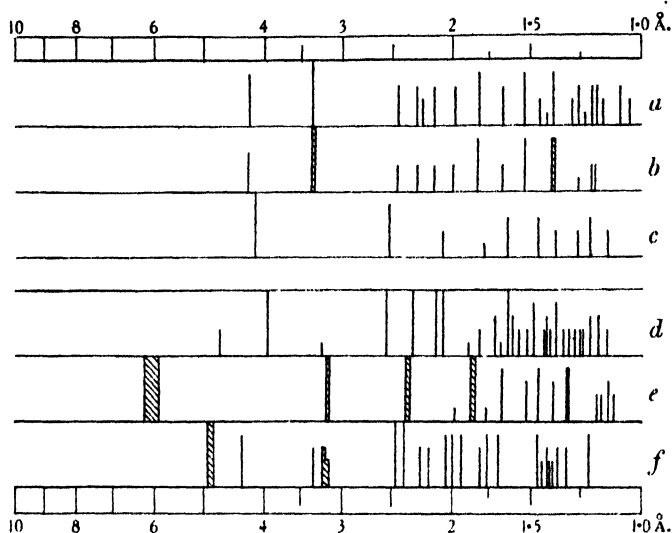


Fig. 1. X-ray data for (a) Quartz, data from Nagelschmidt (1934). (b) Quartz $< 0.2 \mu$ diam., ground under toluene and centrifuged in acetone. (c) Cristobalite, data from Wyckoff (1922). (d) Diaspore from Chester, Massachusetts. (e) Boehmite (Bauxite), unknown locality. (f) Hydrargillite from Richmond, Massachusetts.

states, without giving any experimental data, that hydrargillite is a major component of the clay fraction of many tropical soils from Brazil. Our own preliminary experiments seem to show that boehmite is not completely dissolved by one Truog treatment, though the material used was not a soil colloid but finely ground boehmite, which according to its X-ray diagram was free from diasporite and hydrargillite. We have also found hydrargillite together with kaolinite and other minerals in a concretion from a Malayan soil (Department of Agriculture Experimental Farm, Serdang). The hydrargillite was characterized by its X-ray diagram, which disappeared completely after the sample had been subjected to a Truog treatment.

Oxides and hydroxides of iron

The following oxides and hydroxides of iron are known:

		Refractive indices
1. $\alpha\text{-Fe}_2\text{O}_3$	Hematite	2.9-3.2
2. $\gamma\text{-Fe}_2\text{O}_3$	γ -iron oxide	?
3. $\alpha\text{-FeOOH}$	Goethite or limonite	2.2-2.4
4. $\gamma\text{-FeOOH}$	Lepidocrocite	1.9-2.5

Dehydration and heating curves for the hydroxides have been described by Posnjak & Merwin (1919), Kurnakow & Rode (1928), Hüttig & Garside (1929) and Hüttig & Zörner (1931). X-ray data for hematite are given by Brill (1933), for $\gamma\text{-Fe}_2\text{O}_3$ by Thewlis (1931), and for all the above compounds by Boldyrev (1938). X-ray diagrams and their variation with crystal shape are shown by Böhm (1928), and our data are given in Fig. 2, *a*, *c*. All compounds except $\gamma\text{-Fe}_2\text{O}_3$ are known as natural minerals, but lepidocrocite is rare. The refractive indices of the iron hydroxides are so high that they cannot be measured with the usual immersion liquids, and the use of melts of high refractive index would probably decompose the hydroxides. The dehydration data show that nearly all water is lost below 300° C., whereas the aluminium hydroxides lose the whole of their water only at about 400° C.

Goethite, characterized by its X-ray diagram which disappeared after a Truog treatment, has been found in a number of colloids from American soils by Alexander & Hendricks (1938). Through the courtesy of Dr Alexander¹ we have received a sample of the Cecil colloid, C horizon, for which a complete chemical analysis has been published by Byers *et al.* (1935). Powder diagrams of this colloid before and after a Truog treatment, Fig. 2, *f*, *g* respectively, show less lines for the treated material, and in Fig. 2*b* we have plotted the lines removed by the Truog treatment between those for hematite, Fig. 2, *a*, and goethite, Fig. 2, *c*. It can be seen that Fig. 2, *b* contains lines characteristic of both of these minerals, and that the lines of hematite are more prominent. This does not necessarily mean that there is more hematite present than goethite, because the diffracting power of hematite is stronger, and the intensities of the lines could also be affected by differences in grain size and purity of the two minerals. In order to determine the ratio of hematite to goethite, it is better to use the chemical data. Apart from the iron

¹ The writer takes this opportunity of thanking Dr Alexander for putting at his disposal a number of analysed soil colloids, which have been described by Byers, Alexander and Holmes (1935).

minerals, the X-ray diagram reveals only kaolinite, and if this mineral of ideal composition $\text{Al}_2\text{Si}_2\text{O}_5(\text{OH})_4$ is subtracted, the amount of water left is insufficient for all the iron to be present as $\alpha\text{-FeOOH}$. The chemical analysis shows 17.5% of Fe_2O_3 , of which 10.2% could be present as $\alpha\text{-FeOOH}$, with 7.3% remaining as Fe_2O_3 . This, however, requires the further assumption, which is likely but not strictly proved, that no iron is present in an amorphous form.

These results have been reported in some detail, as the estimation of

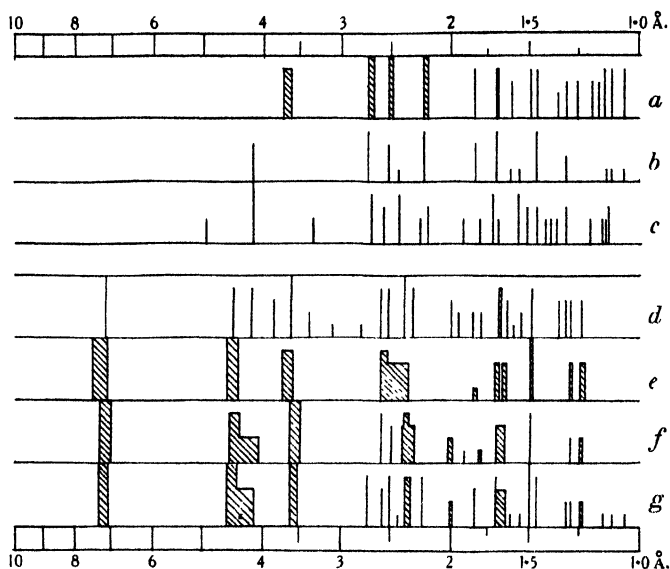


Fig. 2. X-ray data for (a) Hematite from unknown locality. (b) Lines removed by Truog treatment of Cecil colloid, C horizon (b-g-f). (c) Goethite, unknown locality. (d) Kaolinite data from Nagelschmidt (1934). (e) Halloysite from Angleur, Belgium. (f) Cecil C colloid after Truog treatment. (g) Cecil C colloid before Truog treatment.

the different forms of iron oxides may be important from the point of view of phosphate fixation. Detailed dehydration curves would help further to confirm the conclusions based on X-ray and chemical data. It must be remembered that quantitative estimates based on the intensities of X-ray diffraction lines alone could only be obtainable after much careful standardizing.

Both goethite and hematite together with kaolinite have been observed by us in several other soil colloids from India, but these iron minerals have so far not been found to occur in a mixture with montmorillonite or beidellite. This may be due to the fact that kaolinite cannot

incorporate iron within its crystal lattice, whereas minerals of the montmorillonite type can contain up to 30% of Fe_2O_3 (nontronite), but our experience is far too limited at present to establish such conclusions.

Kaolinite-halloysite group

This group includes the following minerals: kaolinite, anauxite, nacrite, dickite, halloysite and hydrous halloysite.¹ X-ray, chemical, optical and dehydration data for these minerals have been given by Ross & Kerr (1930, 1934) and the crystal structures have been discussed by Gruner (1933), Hendricks (1938 *a, b, c*) and others. The chemical composition varies widely; anauxite has a ratio of $\text{SiO}_2:\text{Al}_2\text{O}_3$ of nearly 3, whereas for some halloysite samples this ratio is as low as 1.7. The majority of analysed samples, however, correspond fairly well to the ratio $\text{SiO}_2:\text{Al}_2\text{O}_3=2$. A good summary of experimental data is given by Engelhardt (1937 *a*). The refractive indices of kaolinite (1.560–1.566) are somewhat higher than those of halloysite (1.52–1.55), and only those of halloysite vary with the water content (Mehmel, 1937). The double refraction of kaolinite is weak but distinct, whereas halloysite usually shows no double refraction. X-ray diagrams of kaolinite and halloysite are shown in Fig. 2, *d, e*. Both minerals show strong basal reflexions at 7.2 and 3.6 Å.

Antipov-Karataev & Brunovsky (1936) claim to have found nacrite and dickite in several soil colloids, but their X-ray data are not convincing, and their findings have been questioned by Noll (1938). Kaolinite and halloysite, on the other hand, have often been found in soil colloids. It is quite easy to differentiate the X-ray diagram, dehydration curve or optical properties of a well-crystallized sample of kaolinite from the corresponding data for halloysite, as can be seen from the data given by Ross & Kerr (1934), but soil colloids often present great difficulties. As an example we show in Fig. 2, *f*, X-ray data for the American Cecil colloid, C horizon, after it had been subjected to a Truog treatment. It is intermediate between the kaolinite and halloysite diagrams. Aggregate diagrams of this colloid show only the strong basal reflexions common to kaolinite and halloysite.

Hydrated halloysite with a basal spacing of 10.3 Å has, as far as the writer is aware, never been observed in clays or soil colloids, but this may be due to the fact that the material had at some stage been irreversibly dehydrated to halloysite. The writer has shown (1934) that some halloysite X-ray diagrams represent a gradual transition to the kaolinite

¹ Nomenclature according to S. B. Hendricks (1938 *a*).

diagram, and it seems that all known data are consistent with the explanation then put forward that the difference between kaolinite and halloysite may be due to the size of the single crystallites. Under these circumstances the differentiation between the two minerals is arbitrary and, moreover, does not lead to any useful results. The main difference between the two minerals is that the base exchange capacity is higher for halloysite than for kaolinite. This again may be a grain-size effect, as suggested by the work of Grim & Bray (1936). There are at present not sufficient data available for correlating the grain size and base exchange capacity of kaolinite or halloysite. The subdivision of a soil colloid rich in kaolinite, such as the American Cecil colloid, into different grain-size groups, after removing iron oxide and hydroxide, would probably give interesting results on this question.

Montmorillonite group

This group includes the minerals montmorillonite, beidellite, nontronite, magnesian bentonite and probably in part saponite and bowlingite. The variability in chemical composition is very large indeed, and can be explained by isomorphous replacements, as described by Gruner (1935), Marshall (1935*b*) and the writer (1938). The refractive indices vary with the chemical composition and also with the water content and with the immersion liquid used, as shown by Correns & Mehmel (1936) and by van Baren (1936). The double refraction, generally of the order of 0.02, does not seem to be affected by these changes.

The members of this group are characterized by the fact that they contain large amounts of water which is reversibly taken up or released according to temperature and relative humidity. Hofmann *et al.* (1933) have shown that, with changes in the water content, the crystal lattice expands or shrinks reversibly in the direction perpendicular to the layers of the crystal structure. The amount of water held and the corresponding basal spacing depend under equilibrium conditions largely upon the exchangeable cation. Unpublished experiments on supercentrifuged bentonite fractions showed that for the finest fraction at 50% relative humidity and room temperature 30% water was present on an ignited basis and the basal spacing was 15 Å, if calcium or magnesium were the exchangeable ions, but that under the same conditions only 13.5% water was present and the basal spacing was 12 Å, if potassium was the exchangeable ion. Bentonite, saturated with sodium or hydrogen, took an intermediate position. Similar values for the water content have been given by Thomas (1928) for the "colloid 1296".

X-ray powder data are given in Fig. 3, *a-d*. It can be seen that members rich in trivalent iron or magnesium can be differentiated from those rich in aluminium and silicon, as the unit cell for the latter is somewhat smaller. This, however, applies only to the pure minerals, and has not yet been observed in work on soil colloids. The water content affects the position and intensities of the basal reflexions in the X-ray diagrams, but not the other reflexions. This variation of the basal spacing with varying water content is the best characteristic for members of the montmorillonite group. Samples which are either wetter or drier than corresponds to air-dry equilibrium conditions must be examined in sealed capillaries or in cameras, in which the relative humidity can be

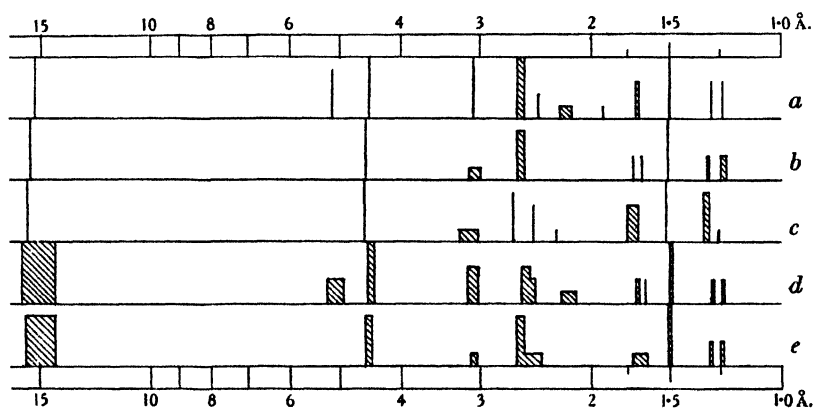


Fig. 3. X-ray data for (*a*) Montmorillonite; (*b*) Nontronite; (*c*) Magnesian bentonite (data from Nagelschmidt (1938)). (*d*) Bentonite <30 μ diam., isolated by supercentrifuging. (*e*) Barnes colloid, B horizon, after removal of calcite. Samples (*d*) and (*e*) saturated with calcium.

varied. Such a camera has been described by Bradley *et al.* (1937). One possible complication must not be overlooked. Giesekeing (1939) has shown that montmorillonite samples, saturated with large complex organic cations, fail to show this variation of basal spacing with water content, and it is possible that soil colloids rich in organic matter might behave similarly. No instance is known to the writer in which a soil colloid containing a member of the montmorillonite group did not show the characteristic variation in basal spacing with varying water content, but the bulk of the organic matter had been removed from all soil colloids so far investigated.

A strong X-ray reflexion at about 15 Å is usually taken to indicate montmorillonite, but such a reflexion may be due to chlorite, with a

strong basal reflexion at 14.2–14.6 Å, which would, of course, not change its position with varying water content. On powder and aggregate diagrams for a member of the montmorillonite group the 15 Å reflexion occurs only if the sample is at 40–60% relative vapour pressure, and is saturated with either calcium or magnesium. If the sample is saturated with potassium, ammonium, hydrogen or sodium, the reflexion may be wide and its centre may correspond to a spacing of 12–13.5 Å, but it will still vary its position with water content.

The effect of varying grain size upon the properties of bentonite has been studied by Hauser & Reed (1937) who showed that the chemical composition, base exchange capacity and X-ray powder diagram are the same for particles with equivalent diameters of 15–90 m μ . Similar experiments carried out in this laboratory confirm the observations of Hauser & Reed for a somewhat wider range of particles of approximately 40–800 m μ equivalent diameter, and it may be added that the dehydration curve and refractive indices also do not vary noticeably within these size limits.

A typical dehydration curve for bentonite saturated with calcium and in equilibrium with an atmosphere of 50% saturation is shown in Fig. 4, *a*. The water held reversibly is lost below 300°, and the loss of water between 350° and 600° C. corresponds to the loss of the lattice hydroxyl groups.¹ Other dehydration data are collected by Engelhardt (1937*a*).

The presence of montmorillonite, beidellite or nontronite in soil colloids has been reported for many soils from different climatic zones. Hendricks & Fry (1930), Kelley *et al.* (1931), Jacob *et al.* (1935), Antipov-Karataev & Brunovsky (1936), Correns & Schlünz (1936), Engelhardt (1937*b*), Schachtschabel (1937), Clark *et al.* (1937), usually on X-ray evidence, but adequate experimental data are rarely given. An exception is the full description by Kelley *et al.* (1939) of montmorillonite in some samples of the Susquehanna Profile, where dehydration, optical and chemical data support the X-ray evidence. We have found a member of the montmorillonite group as a major constituent of the colloid from the B₂ horizon of the American Barnes soil (cf. Byers *et al.* (1935), p. 6), which is a typical soil of the Chernozem group. The X-ray diagram of an air-dry Ca-saturated sample after removal of calcite is given in Fig. 3, *e*.

¹ The writer had previously stated (1938), p. 143, that published dehydration data did not entirely confirm the montmorillonite formula $\text{Al}_2\text{Si}_4\text{O}_{10}(\text{OH})_2 \cdot n\text{H}_2\text{O}$, but the dehydration data for the supercentrifuged bentonite fractions show good agreement with this formula.

Wet and dry samples show the characteristic shift of the basal reflexion from 10.4 Å for material dried at 350° C. to 18 Å for wet material. The

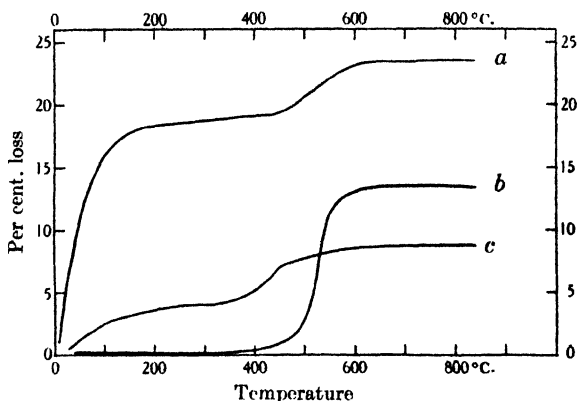


Fig. 4. Dehydration curves by the method of intermittent heating. (a) Montmorillonite, calcium-saturated supercentrifuged bentonite. (b) Kaolinite, data from Ross & Kerr (1934). (c) Illite, data from Grim, Bray & Bradley (1937).

colloid contains about 5% calcium carbonate in the form of calcite, and a Truog treatment removed 20% of the colloid. Truog treatment of supercentrifuged bentonite fractions resulted in the loss of 10–15% of bentonite, which is in good agreement with the result on the Barnes colloid.

Mica group

The group of micas has been studied extensively by mineralogists, and the chemical variations have been reviewed by Niggli (1937). Although it is known that mica forms an important part of many soil colloids, little is yet known about the variability in chemical composition and physical properties of such mica. The most extensive data are given by Grim *et al.* (1937) who isolated mica from slates and argillaceous sediments and determined its chemical composition, dehydration curve, optical properties and X-ray powder diagram. They proposed the name illite for mica of this type. The refractive indices vary, according to these authors, from 1.56 to 1.61, the double refraction is of the order of 0.03, and one of their dehydration curves is shown in Fig. 4, c. The part above 500° C. is similar to the dehydration curve of montmorillonite. Chemical, dehydration and X-ray data for similar materials are given by Maegdefrau & Hofmann (1937). The terms hydrous mica or hydromica, sericite, potassium-bearing clay, and Ordovician bentonite may cover similar

materials. The X-ray data given in the literature are presented in Fig. 5, *b, c*. Mica always shows strong basal reflexions at 10 and 3.34 Å and a weak basal reflexion at 5 Å. The X-ray diagram contains somewhat more lines than the montmorillonite and halloysite diagrams.

Mica is often found in mixture with kaolinite, and heating to 500° C. does not affect the X-ray diagram of mica, although it completely

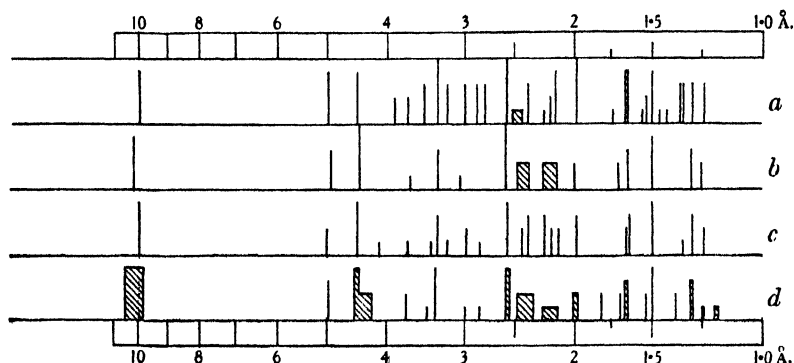


Fig. 5. X-ray data for (*a*) Muscovite, data from Nagelschmidt (1937). (*b*) Illite, data from Grim *et al.* (1937). (*c*) Illite, data from Maegdefrau & Hofmann (1937). (*d*) Miami colloid, B horizon (cf. Byers, Alexander & Holmes (1935)).

destroys the kaolinite diagram. In this way it is possible to detect small quantities of mica in the presence of large quantities of kaolinite. The presence of hydrous mica in a number of American soil colloids has been described by Alexander & Hendricks (1938). We found such mica as the main component of the colloid from the B horizon of the American Miami silt loam, which is characteristic for the grey-brown podsollic soil group (cf. Byers *et al.*, 1935). The X-ray diagram of this colloid is shown in Fig. 5, *d*.

Other minerals

X-ray data for calcite have been given by the writer (1934), and for various other carbonates and silicates by Boldyrev (1938). Members of the group of palygorskites may exist in soil colloids, and the literature with regard to this group has recently been reviewed by Lapparent (1939). It is possible that other minerals exist in soil colloids; but our knowledge at present does not seem to justify the listing of any details concerning such minerals.

SUMMARY

X-ray, optical, dehydration and chemical methods in use for the identification of minerals in soil colloids are discussed with special regard to their limitations. These are mainly due to uncertainties about the variation of physical properties of standard minerals with decreasing grain size and the possible existence and importance of amorphous material. The aggregate method in X-ray analysis, which is specially important for soil colloids, is described. Various techniques for dehydration and optical analysis are discussed, and it is concluded that they are useful only when used in combination with X-ray data. The advantages of combining various chemical methods with X-ray analysis are pointed out.

Standard data are given for a number of minerals, and the evidence for their occurrence in soil colloids is reviewed. These minerals are quartz, cristobalite, oxides and hydroxides of iron and aluminium, minerals of the kaolinite, montmorillonite and mica groups.

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NOTE ADDED IN PROOF-READING

A detailed study of heating curves of clay minerals has been published by Norton, F. H. (1939), *J. Amer. ceram. Soc.* **22**, 54.

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NUTRITION OF THE BACON PIG

IV. THE INFLUENCE ON GROWTH, CONFORMATION AND CARCASS QUALITY OF INCLUDING MEAT MEALS OF WIDELY-DIFFERING FAT CONTENT IN THE RATIONS OF BACON PIGS

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INTRODUCTION

THE amount of oil in the diet and its degree of unsaturation are known to exert an important effect on the nature of the fat deposited in the body of the growing pig, foods of high oil content tending to give rise to bacon carcasses containing fat of an undesirably soft and unsaturated character. For this reason, authorities on pig nutrition are agreed on the desirability of excluding from the dietary of the bacon pig all foods containing more than a small percentage of oil. It has been stated that, in order to avoid the danger of producing carcasses with soft fat, the meal ration of the fattening pig should be made up so as to contain no more than about 3% of oil.

This prejudice against the use of feeding stuffs rich in *oil* has been transferred, somewhat unquestioningly perhaps, to feeding stuffs rich in *fat*. Feeding meat meal, for example, contains normally from 8 to 10% of fat, and manufacturers complain of the difficulty of securing sales of this product for pig-feeding on account of the view generally held that its high fat content would occasion the production of soft fat in the resultant bacon or a carcass with an excessive amount of fat. To meet this prejudice, therefore, the meat meal as ordinarily produced is frequently submitted to a process of de-greasing with petroleum benzine at about 200° F. so as to give a meat meal containing about 3% of fat. This procedure, however, not only adds to the cost of the manufacture of meat meal, but may actually lead to a distinct lowering of the digestibility of the product (Woodman & Evans, 1937).

Two points should be kept in mind when considering the possible effect of the fat of meat meal on the character of the carcass fat: (1) The meat meal fat is of a relatively saturated character, its iodine value of

approximately 53 being very much lower than the corresponding values for the oil in white fish meal or maize, namely, about 155 and 115 respectively. Since the iodine value of the back fat in bacon carcasses of good, firm quality is in the neighbourhood of 65, and that of the belly fat is about 64, there appears on prior grounds no reason to suppose that the inclusion in the diet of meat meal fat, with an iodine value as low as 53, should lead to an increase in the degree of unsaturation of the body fat. (2) Meat meal would rarely form more than 10–12% of the ration of bacon pigs, and the fat in this feeding product would therefore never constitute more than a minor ingredient of the diet. A ration composed of 65 parts of barley meal, 25 parts of weatings, and 10 parts of meat meal (10% fat) would, for example, contain about 3.1% of ether extract, of which no more than 1% would consist of meat fat. The position is different, however, when a cereal such as maize, containing a moderate proportion of unsaturated oil, is used to replace barley meal. A ration of 65 parts of maize, 25 parts of weatings and 10 parts of white fish meal would contain as much as about $4\frac{1}{2}$ % of a highly unsaturated type of oil, and the “softening” effect of such a diet can readily be understood.

In view, therefore, of the low iodine value of the fat in meat meal and the relatively small proportion of this feeding product usually included in pig rations, it seemed justifiable to assume that the prejudice against the use of meat meal containing 8–10% of fat might have no real foundation. It was decided to put the matter to the test of experiment, and it is the purpose of this paper to describe two separate feeding trials in which the effect on growth and carcass quality of feeding three grades of meat meal of widely-differing fat content was investigated.

TRIAL I (MARCH–AUGUST 1936)

The feeding treatments and the lay-out of the experiment

The reader is referred to a previous publication for details of the methods of manufacture of the three grades of meat meal and for an account of experiments in which the composition and digestibility of the meat meals were determined (Woodman & Evans, 1937). The average composition of the grades used in the present trial is shown in Table 1. It should be pointed out that the grade A meat meal, with a fat content of 17.3%, is not sold for the purpose of pig-feeding, but was included in this trial so that the effect of meat meal fat on carcass quality might be tested under more stringent conditions than are ever likely to be encountered in feeding practice.

Table I. *Average composition of feeding stuffs*

	Grade A meat meal %	Grade B meat meal %	Grade C meat meal %	Barley meal %	Weatings %	Lucerne meal %
Moisture	8.34	9.52	7.60	14.50	14.46	10.00
Crude protein	60.84	64.78	66.24	9.79	16.29	18.88
Ether extract*	17.25	10.03	2.93	2.51	4.57	5.52
N-free extractives	2.60	2.21	3.95	67.50	57.55	38.98
Crude fibre	—	—	—	3.64	4.32	16.28
Ash	10.97	13.46	19.28	2.06	2.81	10.34
Lime (CaO)	3.58	4.22	6.88	—	—	—
Phosphoric acid (P ₂ O ₅)	3.66	4.09	5.78	—	—	—
Chlorine (Cl ₂)	1.19	1.80	1.42	—	—	—
True protein	46.21	49.17	51.12	—	—	—
"Amides"	14.63	15.61	15.12	—	—	—
Digestible organic matter	74.36	71.96	64.60	—	—	—
*Iodine value of fat	51.9	51.8	54.5	—	—	—

The feeding treatments are summarized in Table II. It will particularly be noted that the tests were carried out with rations containing amounts of meat meal such as would be used in commercial feeding practice, namely, 10% up to 150 lb. live weight and 5% from 150 lb. to slaughter at about 200 lb. live weight.

Table II. *Summary of feeding treatments*

Parts by weight	Treatment A (high-fat meat meal)	Treatment B (medium-fat meat meal)	Treatment C (low-fat meat meal)
Up to 150 lb. L.W.:			
Barley meal	55	55	55
Weatings	33	33	33
Lucerne meal	2	2	2
Meat meal	10	10	10
Ground chalk	1	0.8	0.5
150-200 lb. L.W.:			
Barley meal	60	60	60
Weatings	33	33	33
Lucerne meal	2	2	2
Meat meal	5	5	5
Ground chalk	1.25	1.15	1
Common salt	0.25	0.25	0.25

The experimental procedure was similar to that adopted in the first trial of this series (Woodman *et al.* 1936). Thirty Large-White pigs, representing five litters, were included in the individual-feeding lay-out, in which each of the five pens contained six pigs, three hogs and three gilts, from a given litter. The three feeding treatments, A, B and C, were applied to the three hogs and the three gilts in each pen, so that in all there were ten separate comparisons of the influence of the feeding treatments. The comparison was also carried out by the group-feeding technique on three groups of nine pigs of the Large-White breed, the usual

precautions being observed in the selection of the animals composing the three groups.

The distribution of the pigs into pens and groups was made on the basis of their live weights on 7 March, and by the 15th of this month all the pigs had been brought on to the full experimental rations. The animals were weighed on the mornings of 23, 24 and 25 March and the means of the three weighings taken as the initial weights in the trial.

PRE-SLAUGHTER RESULTS (TRIAL I)

The meal supply was scaled in relation to the live weight of the pigs, rising from 1.1 lb. at 20 lb. to a maximum of 7 lb. per day at 200 lb.

Table III. *Live-weight gains and meal consumption of individually-fed pigs over experimental period 24 March to 30 June (14 weeks)*

Feeding treatment	No. and sex of pig	Live weight on 24 March lb.	Live weight on 30 June lb.	Total meal consumed lb.
Pen I (sow 229)				
A	G 1582	50½	180	453.60
B	G 1579	48½	184½	453.25
C	G 1583	47	171½	428.05
C	H 1584	42	151½	393.75
B	H 1585	55½	191½	480.90
A	H 1580	47	162	421.75
Pen II (sow 436)				
B	G 1587	34	124	308.10
C	G 1589	37½	137½	350.00
A	G 1591	48	181	446.25
C	H 1595	46½	171½	437.15
A	H 1594	45	176½	437.75
B	H 1592	41	156	395.40
Pen III (sow 334)				
C	G 1549	50	160½	404.65
A	G 1558	45½	167	425.95
B	G 1555	41	166	409.85
B	H 1547	51	185	466.55
C	H 1548	55	183	474.25
A	H 1545	49	179½	452.90
Pen IV (sow B 1)				
C	G 4	42	159	404.15
A	G 5	40½	186½	425.55
B	G 6	39½	171½	407.90
A	H 3	39	163	399.25
B	H 1	55½	190½	477.20
C	H 2	46	165	423.85
Pen V (sow C 1)				
B	G 16	42	160	393.39
A	G 14	46½	175	430.15
C	G 15	42½	158½	395.70
B	H 18	53½	188	471.80
C	H 19	47	138	382.45
A	H 17	51	187½	462.70

live weight (for precise details, see Woodman *et al.* 1936). In Table III, which shows the lay-out of the individual-feeding experiment, are recorded the initial and final live weights of the animals, together with their food consumption between 24 March and 30 June, on which day the first consignment of pigs was ready for dispatch to the bacon factory. Full records were still kept, however, until every pig had reached 200 lb. live weight. Table IV shows the average live weights of the pigs, as determined at weekly intervals, under the three feeding treatments.

Table IV. *Average weekly live weights and total meal consumption of pigs under different feeding treatments (24 March to 30 June)*

Treatment ...	Individually-fed pigs			Group-fed pigs		
	A	B	C	A	B	C
No. of pigs ...	10	10	10	9	9	9
	lb.	lb.	lb.	lb.	lb.	lb.
24 March	46.20	46.15	45.55	50.55	51.83	51.00
31 "	51.60	51.92	50.85	55.78	57.39	56.83
7 April	57.40	57.36	55.70	61.89	62.94	62.17
14 "	64.25	63.86	61.70	68.22	69.61	68.44
21 "	72.70	72.07	69.85	75.50	77.39	76.44
28 "	81.85	80.41	77.45	83.61	86.22	84.56
5 May	91.70	89.73	86.05	92.11	94.61	93.33
12 "	101.20	98.73	94.35	100.33	104.16	101.61
19 "	110.90	108.28	103.40	108.77	113.17	110.72
26 "	120.90	118.44	112.20	118.22	123.22	120.61
2 June	131.35	128.38	121.30	127.89	133.44	129.67
9 "	141.75	139.10	130.50	137.90	143.67	140.11
16 "	152.10	150.26	140.60	149.00	155.11	151.17
23 "	164.75	161.48	150.80	159.83	165.28	162.39
30 "	175.80	171.70	159.60	170.11	176.11	172.28

Meal consumption from 24 March to 30 June (average per pig)

Treatment	Grade of meat meal	Individually-fed	Group-fed
		pigs (lb.)	pigs (lb.)
A	High-fat	435.58	438.10
" B	Medium-fat	426.43	448.70
" C	Low-fat	409.40	442.70

Comments on Tables III and IV

The observed differences in live-weight increase and meal consumption over the 14 weeks of the comparison are:

(1) Individually-fed pigs				
Treatment	A	B	C	S.E.
Grade of meat meal	High-fat	Medium-fat	Low-fat	
Average L.W.I. over period (lb.)	129.60	125.55	114.05	3.88
Average meal consumption (lb.)	435.6	426.4	409.4	10.12
(2) Group-fed pigs				
Average L.W.I. over period (lb.)	119.56	124.28	121.28	4.20
Average meal consumption (lb.)	438.1	448.7	442.7	—

The analysis of variance (see Woodman *et al.* 1936) reveals that there was no significant difference between the live-weight gains of the pigs on the A and B feeding treatments, but that in the case of the individually-fed pigs, the pigs on the C diet, containing the meat meal of lowest fat content, made significantly poorer gains than the A and B pigs over the 14 weeks of the comparison. This finding remains significant when the results are corrected for differences in the initial live weights of the pigs under the three feeding treatments.

The poorer gains of the individually-fed C pigs might be ascribed in part to the much lower fat content and somewhat lower digestibility of the grade C meat meal. If this be the whole explanation, however, it is difficult to account for the fact that the A and B pigs showed such small differences in mean live-weight gains, since the A meat meal was very much richer in fat than the meat meal included in the B treatment. In any case, it would scarcely be expected that these differences in the meat meals, which formed such a minor part of the total rations, would be the sole cause of such pronounced differences of live-weight increase as were manifested between the A and C pigs and the B and C pigs of the individual-feeding lay-out.

Further, if these differences in live-weight increase were to be attributed wholly to the influence of feeding treatment, it would be anticipated that differences of a like nature would be discernible in the results for the group-fed pigs. It will be observed, however, that the effect is entirely absent, such small differences as exist being entirely without statistical significance.

A study of the day-to-day records of the trial reveals that among the 10 individually-fed pigs in the C treatment were four pigs that gave the attendant a great deal of trouble during the course of the experiment. In particular, hog 19 (pen V) was a very poor "doer"; it was a slow eater and was inclined to be "blown" after meals; it was frequently quite off its feed and was subject to attacks of scour; during the early part of the trial it became very weak on the legs, and although it showed an all-round improvement during the later stages before attaining 200 lb. live weight, its general record of health and appetite was very unsatisfactory. During the 14 weeks' comparison it gained only 91 lb., compared with an average of about 123 lb. for all the pigs in the individual-feeding lay-out. In addition to this pig, gilt 1589 (pen II), gilt 1549 (pen III) and gilt 15 (pen V) all gave rise to some anxiety in relation to condition and feeding at various times in the experiment, and it is felt that the relatively poor average gain among the individually-fed C pigs is to be ascribed to the

inclusion in this treatment of a number of animals that were found, as the trial proceeded, to be below the general level of constitution and thriftiness rather than to any significant differences between the nutritive values of the three diets under test. This complication serves to illustrate the type of unforeseen difficulty that may arise in work of this nature.

Table V. *Treatment averages for 14 weeks of comparison*

Treatment	Grade of meat meal	Individually-fed pigs			Group-fed pigs			
		Range of L.W. lb.	lb meal consumed per pig	lb. L.W.I. per day	lb meal per lb. L.W.I.	Range of L.W. lb.	lb. meal consumed per pig	lb. L.W.I. per day
A	High-fat	46.20-175.80	435.6	1.32	3.36	50.55-170.11	438.1	1.22
B	Medium-fat	46.15-171.70	426.4	1.28	3.40	51.63-176.11	448.7	1.26
C	Low-fat	45.55-159.60	409.4	1.16	3.59	51.00-172.28	442.7	1.24

The results over the 14 weeks of comparison are summarized in Table V so as to bring out the effects of feeding treatment in respect of both the rate of live-weight gain and the efficiency of food conversion. Only minor differences characterize the performances of the group-fed pigs on the three types of ration, a finding that applies also to the differences between the individually-fed pigs on treatments A and B. The probable meaning of the poorer results for the individually-fed C pigs has already been discussed. The figures also demonstrate the somewhat greater thriftiness of the pigs fed as individuals in comparison with the group-fed pigs, a finding that has been noted consistently in this series of trials.

A summary of the records of the pigs right up to slaughter at 200 lb. live weight is given in Table VI.

Table VI. *Treatment averages for the whole period up to 200 lb. live weight*

Treatment	Individually-fed pigs				Group-fed pigs			
	Total lb. L.W.I.	No. of days on experiment	lb. L.W.I. per day	lb. meal per lb. L.W.I.	Total lb. L.W.I.	No. of days on experiment	lb. L.W.I. per day	
A	153.80	112.4	1.37	3.47	149.45	117.3	1.27	
B	153.85	116.2	1.33	3.53	148.17	113.5	1.30	
C	154.45	123.8	1.25	3.73	149.00	115.0	1.30	
S.E.		3.21	0.083	0.056		N.S.	N.S.	

It is clear from Table VI that, considering the results of the individually-fed pigs for the whole period of feeding, there are still no significant differences between the results for the pigs on treatments A and B. It will be observed that although the C pigs showed a distinctly poorer average rate of live-weight gain than the A and B pigs, the difference fails to

reach statistical significance. In this respect, therefore, the findings for the complete experiment are not quite consistent with those for the first 14 weeks of the comparison, at the end of which the average live weight of the C pigs (159.6 lb.) was significantly smaller than the corresponding figures for the A and B pigs. During the further period of the trial, however, hog 19 and the other troublesome animals among the C pigs began to feed more satisfactorily and to show normal gains, so that the slightly better results for the C pigs over the experiment as a whole is in reality a reflexion of this improvement in general condition and thriftiness displayed by the pigs at the heavier weights. The C pigs, however, were still significantly behind the A and B pigs in regard to efficiency of conversion of meal into live-weight increase. The results in Table VI for the group-fed pigs point very definitely to the conclusion that the animals on the three different feeding treatments displayed almost equal average rates of growth over the whole period of feeding.

POST-SLAUGHTER RESULTS (TRIAL I)

The reader is referred to the first publication in this series for a detailed account of the technique of the post-slaughter work (Woodman *et al.* 1936). It will not be feasible, from considerations of space, to record the whole of the measurements made on every carcass, and only the treatment averages, together with the results of the analysis of variance, will therefore be given.

Table VII. *Effect of feeding treatment on thickness of back fat and belly streak (treatment averages)*

Treatment	Grade of meat meal	Back fat*				Belly streak†			
		(a) mm.	(b) mm.	(c) mm.	Mean mm.	(a) mm.	(b) mm.	(c) mm.	Mean mm.
Individually-fed pigs									
A	High-fat	51.4		33.8	36.9	26.1	36.5	42.3	35.0
B	Medium-fat	51.8	27.2	35.3	38.1	26.6	37.0	43.1	35.6
C	Low-fat	52.3	26.6	36.7	38.5	27.5	38.8	44.2	36.8
S.E.					0.75				1.16
Group-fed pigs									
A	High-fat	50.1	25.7	35.0	36.9	26.7	36.4	43.1	35.4
B	Medium-fat	50.7	24.4	33.8	36.3	26.2	35.1	41.6	34.3
C	Low-fat	50.7	25.3	33.3	36.4	26.8	36.6	41.7	35.0
S.E.					1.09				0.85

* As measured (a) at the thickest point at the shoulder, (b) at the thinnest point along the back and (c) opposite the junction of the third and fourth vertebrae from the curve.

† As measured (a) opposite the curve, (b) opposite the junction of the fourth and fifth vertebrae from the curve and (c) at a distance below (b) equal to the distance from (a) to (b).

Comments on Table VII

The figures in Table VII show very conclusively that differences in feeding treatment have been entirely without significant effect on the back fat and belly streak measurements. There is not the slightest evidence that the use, in normal amounts, of meat meal A, containing as much as 17.3% of fat, produced a greater thickness of back fat or belly streak than was produced on rations containing the same amounts of meat meal C, with only 2.9% of fat. The same conclusion, in respect of back fat, is arrived at from a consideration of the separate measurements of the inner and outer layers of back fat. The figures are given in Table VIII.

Table VIII. *Effect of feeding treatment on thickness of inner and outer layers of back fat (treatment averages)*

Treat- ment	Grade of meat meal	Inner back fat*				Outer back fat*			
		(a)	(b)	(c)	Mean	(a)	(b)	(c)	Mean
		mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
(1) Individually-fed pigs									
A	High-fat	38.6	15.2	21.0	24.9	12.8	10.2	12.8	11.9
B	Medium-fat	37.9	16.7	22.8	25.8	13.9	10.5	12.5	12.3
C	Low-fat	38.6	15.9	23.3	25.9	13.7	10.7	13.4	12.6
(2) Group-fed pigs									
A	High-fat	35.6	15.1	20.7	23.8	14.5	10.6	14.3	13.1
B	Medium-fat	37.9	14.6	22.0	24.8	12.8	9.8	11.8	11.5
C	Low-fat	37.0	15.8	21.3	24.7	13.7	9.5	12.0	11.7

* See footnotes to Table VII.

Table IX. *Effect of feeding treatment on size and leanness of typical rashers (treatment averages)*

Treatment	"Warm" carcass weight lb.	Belly rasher*			Mid-back rasher*			Complete rasher*		
		Total area† sq. cm.	Area of		Total area† sq. cm.	Area of		Total area† sq. cm.	Area of	
			Lean sq. cm.	Fat sq. cm.		Lean sq. cm.	Fat sq. cm.		Lean sq. cm.	Fat sq. cm.
(1) Individually-fed pigs										
A	159.3	91.50	25.36	63.68	126.54	38.90	85.40	218.04	64.26	149.06
B	160.5	91.58	26.31	62.53	127.58	38.39	86.57	219.16	64.70	149.10
C	160.3	92.01	27.61	60.99	131.14	40.17	88.46	223.15	67.78	149.45
S.E.		2.13	1.03	1.98	3.21	1.20	2.66	4.82	1.89	3.93
(2) Group-fed pigs										
A	160.2	89.98	29.38	58.03	127.10	42.48	82.01	217.08	71.86	140.04
B	158.5	85.01	27.20	54.77	124.58	42.26	79.72	209.59	69.46	134.49
C	159.4	86.55	28.12	55.42	124.53	42.23	79.61	211.08	70.35	135.03
S.E.		2.37	0.96	2.45	2.96	1.38	3.46	4.69	1.94	5.45

* See first publication of this series (Woodman *et al.* 1936) for explanation of these terms.

† Total area minus sum of areas of lean and fat equals area occupied by bone.

Comments on Table IX

The differences between the treatment averages for the total area, the area of fat and the area of lean in the typical rashers are of a minor character when compared with the range of variation within any one treatment. Such differences as exist are entirely without statistical significance. The absence of any effect of feeding treatment may also be demonstrated by expressing the fat and lean as percentages of the area of the complete rasher (see Table X).

Table X. *Fat and lean as percentages of complete rasher*
(treatment averages)

Treatment	Grade of meat meal	Individually-fed pigs		Group-fed pigs	
		Fat (%)	Lean (%)	Fat (%)	Lean (%)
A	High-fat	68.4	29.5	64.5	33.1
B	Medium-fat	68.0	29.5	64.2	33.1
C	Low-fat	67.0	30.4	64.0	33.3

Since, from the standpoint of the consumer, the "eye" muscle, with its large area of lean, is the most important part of the rasher, special attention was devoted to securing the details of its dimensions. These are recorded in Table XI.

Table XI. *Influence of feeding treatment on "eye" muscle measurements* (treatment averages)

"Eye" muscle in mid-back rasher

Treatment	Grade of meat meal	Space within line of connective tissue			"Eye" muscle		Back fat opposite "eye" mm.
		Total area sq. cm.	Lean sq. cm.	Fat sq. cm.	Length cm.	Depth cm.	
(1) Individually-fed pigs							
A	High-fat	34.18	27.43	6.75	7.66	5.41	31.6
B	Medium-fat	35.22	28.10	7.12	7.85	5.51	31.6
C	Low-fat	35.01	27.70	7.31	7.58	5.85	32.4
S.E.		0.85	0.76	0.48	0.13	0.16	1.32
(2) Group-fed pigs							
A	High-fat	35.13	28.79	6.34	7.70	5.78	29.3
B	Medium-fat	35.53	30.52	5.01	7.52	5.90	27.0
C	Low-fat	34.87	28.51	6.36	7.58	6.17	28.8
S.E.		0.93	1.09	0.42	0.20	0.20	1.38

An inspection of the figures in Table XI reveals what is, for this type of work, a remarkably good agreement between the treatment averages for the dimensions of the "eye" muscle. There is no evidence of any significant effect of feeding treatment, a finding that applies also to the thickness of the back fat opposite the "eye" muscle

Table XII. *Influence of feeding treatment on certain post-slaughter measurements (treatment averages)*

Treatment	Grade of meat meal	Farm-fasted L.W.* lb.	L.W. at factory† lb.	"Warm" carcass percentage‡	Length§ cm.	Flares gm.	Filletts gm.	Sides as¶ % of carcass weight
(1) Individually-fed pigs								
A	High-fat	198.3	192.7	82.64	77.8	1626	458	76.44
B	Medium-fat	200.0	195.8	82.07	77.1	1705	471	76.12
C	Low-fat	199.3	193.9	82.67	77.5	1792	471	76.30
S.E.				0.46	0.46	66.4	11.6	0.11
(2) Group-fed pigs								
A	High-fat	199.9	196.0	81.74	78.0	1799	479	76.33
B	Medium-fat	200.3	193.2	82.06	78.4	1578	488	76.03
C	Low-fat	201.2	196.3	81.22	78.5	1772	483	75.92
S.E.				0.35	0.54	105.2	13.5	0.19

* After 24 hr. from previous meal.

† After road transport of fasted pigs about 40 miles to factory.

‡ Without applying the allowance for shrinkage on cooling.

§ As measured from point between first and second ribs to *pubis symphysis*.

|| Total weights of flares and fillets from both sides

¶ Based on weights of trimmed sides before curing.

Comments on Table XII

It is at once evident that differences of feeding treatment have exerted no significant influence on the conformation of the pigs as judged by length, carcass percentage and the weights of the sides expressed as percentages of the carcass weights. The figures for the weights of the flares are of particular interest, since the flare may be regarded as a physiological unit of fatty tissue. It might therefore be expected that the flare weights would constitute a good index of any differences that might result from the use of meat meals of such widely-differing fat content. In the case of the individually-fed pigs, there is a distinct, though not significant, rise in the amount of flare fat on passing from treatment A to treatment C. This trend, however, is the reverse of what would have been expected, since it implies that the weight of flare fat increased as the percentage of fat in the meat meals decreased. The figures for the group-fed pigs also suggest a lack of consistent relationship between the weights of flare fat and the fat content of the meat meals. The treatments A and C, containing the meat meals of highest and lowest fat content respectively, gave almost equal weights of flare fat, whereas treatment B, with the meat meal of medium fat content, gave a distinctly, though not significantly, lower weight of flare fat.

The fillets may be regarded in like manner as physiological units of muscular tissue, and it is therefore of interest to note that the feeding treatments gave rise to no significant differences in respect of fillet weights.

Table XIII. *Influence of feeding treatment on iodine value of carcass fat (treatment averages)*

Treat- ment	Iodine value of meat meal fat	Individually-fed pigs				Group-fed pigs			
		Back fat*	Inner back fat†	Belly fat‡	Flare fat§	Back fat	Inner back fat	Belly fat	Flare fat
A	51.9	66.37	60.20	64.62	53.93	68.77	62.20	65.88	56.40
B	51.8	65.65	59.27	63.41	53.37	67.64	59.69	65.08	54.54
C	54.5	65.69	58.24	63.56	53.13	66.80	59.20	64.01	53.93
S.E.		0.55	0.67	0.71	0.34	0.80	1.11	0.86	0.74

* Taken from gammon end where inner and outer layers merge (bung fat).

† One side from each carcass was cut, after curing, at a point in the back between the fourth and fifth ribs (counting from gammon end) right through to the belly. A cut of bacon about 4 in. thick was then taken. From this, samples of the inner layer of back fat were taken by means of borers of appropriate diameter at a point opposite the "eye" muscle.

‡ Samples were taken at the belly end of the cut obtained as in † and dissected free from lean and outer skin prior to extraction of fat.

§ The lighter flare from each carcass was minced in a special machine and mixed thoroughly before sampling.

Comments on Table XIII

It has already been made clear in the introduction to this paper that one of the main objects of the present trial was to discover whether the inclusion in pig rations, in normal amounts, of a meat meal containing about 10% of fat (meat meal B) would lead to the production of a softer carcass fat than was obtained when extracted meat meal containing only 2.9% of fat (meat meal C) was used. In order to exaggerate the possible softening effect of the meat meal fat, a third meat meal containing 17.3% of fat (meat meal A) was also included in the comparison, although meat meal of this character, with such a high fat content, would not ordinarily come on to the market.

The opinion of the bacon curer himself on the question of carcass quality is naturally of primary importance, since he views the bacon carcass from the standpoint of market suitability. For this reason, an expert factory opinion¹ was obtained in every case following the removal of the cured sides from the chilling room. A summary of these opinions is given in Table XIV.

In considering the results in Table XIV, it should be kept in mind that the bacon carcasses as a whole, irrespective of feeding treatment, were regarded by the factory as being of very satisfactory marketable quality. It was stressed by the factory expert that the category designated "slightly soft" did not by any means represent the objectionable softness or "oiliness" that might result from the excessive feeding of

¹ The writers wish to take this opportunity for expressing their gratitude to Mr W. H. Parr, of the St Edmundsbury Co-operative Bacon Factory, for his valuable help in this connexion.

maize. There would not be the slightest difficulty in selling such a type of carcass. The term "slightly soft" is used merely to indicate that the fat was observably less firm than was the case with the carcasses coming in the "medium firm" category.

Table XIV. *Analysis of factory opinions on quality of carcass fat*

	Treatment	Grade of meat meal	No. of carcasses with fat adjudicated as			
			Very firm	Firm	Medium firm	Slightly soft
A	(19 pigs)	High-fat	1	12	4	2
B	(19 pigs)	Medium-fat	2	14	2	1
C	(19 pigs)	Low-fat	4	13	1	1

It is difficult to escape the conclusion, however, that there is evidence of some slight improvement in carcass-fat firmness on passing from treatment A, with its high-fat meat meal, to treatment C, containing the meat meal of very low fat content. From what has been written already, such differences had little or no significance from the curer's standpoint, and it is important to note that the differences in this respect between treatments B and C, which contained the marketable grades of meat meal, were narrowed down considerably.

Since the usual chemical index of fat firmness is the iodine value of the fat, it is of interest to consider the significance of the figures in Table XIII, in which are recorded the treatment averages for the iodine values of samples of fat taken from four different parts of the carcass (see footnote to Table XIII). The magnitude of the iodine values bears out the factory opinion that the carcasses as a whole were of satisfactory quality from the standpoint of the physical character of the body fat. The results show no significant differences between the treatment averages, although again there is evidence of a slight, though statistically insignificant, trend of improvement in the direction of treatment A to treatment C. It will be observed, however, that the comparison of greatest practical importance, that between treatments B and C, failed to reveal anything but the most minor differences.

TRIAL II (JUNE-DECEMBER 1937)

The possibility that the results of pig-feeding trials may, in some degree, be influenced by the season of the year in which the experiments are carried out is one that must always be kept in mind. Cautiousness in this respect is all the more advisable when the problem under investigation embraces the questions of fat deposition and fat firmness. For this

reason, a repetition of the trial just described seemed very desirable. The first trial lasted from early March to early August, 1936, whilst the second trial was carried out over the period from June to December, 1937.

In Table XV is given the plan of the feeding treatments. The latter differed from those of the first experiment in two minor respects: (i) the lucerne meal was replaced by dried grass meal; (2) all three feeding treatments, up to the stage when the pigs reached 150 lb. live weight, contained 1% of ground chalk instead of amounts varying from 0.5 to 1% (see Table II). The composition of the three new consignments of meat meal are shown in Table XVI.

Table XV. *Summary of feeding treatments*

Parts by weight	Treatment A (High-fat meat meal)	Treatment B (Medium-fat meat meal)	Treatment C (Low-fat meat meal)
Up to 150 lb. l.w.:			
Barley meal	55	55	55
Weatings	33	33	33
Dried grass meal	2	2	2
Meat meal	10	10	10
Ground chalk	1	1	1
150-200 lb. l.w.:			
Barley meal	60	60	60
Weatings	33	33	33
Dried grass meal	2	2	2
Meat meal	5	5	5
Ground chalk	1.25	1.25	1.25
Common salt	0.25	0.25	0.25

Table XVI. *Average composition of feeding stuffs*

	Grade A meat meal %	Grade B meat meal %	Grade C meat meal %	Barley meal %	Weatings %	Dried grass meal %
Moisture	7.20	8.30	10.40	14.80	13.87	7.19
Crude protein	61.20	71.00	73.77	9.26	16.42	17.37
Ether extract*	19.88	9.30	2.02	1.96	4.55	6.40
N-free extractives	0.50	—	0.90	66.93	56.68	39.34
Crude fibre	—	—	—	4.58	5.32	19.65
Ash	11.22	11.40	12.91	2.47	3.16	10.05
Lime (CaO)	3.99	3.59	4.21	—	—	—
Phosphoric acid (P ₂ O ₅)	3.50	3.30	3.88	—	—	—
Salt (NaCl)	2.77	3.93	3.92	—	—	—
True protein	47.16	53.43	54.65	—	—	—
"Amides"	14.04	17.57	19.12	—	—	—
*Iodine value of fat	48.5	51.4	52.6	111.1	120.5	—

PRE-SLAUGHTER RESULTS (TRIAL II)

The lay-out of the individual-feeding trial is shown in Table XVII. Three comparable lots of 10 pigs were also used in group-feeding comparisons. All the pigs in the experiment were of the Large-White breed. The

trial on this occasion did not proceed without set-backs. On 8 September (10th week of experiment) a number of the pigs, distributed over all the feeding treatments, began to show loss of appetite and symptoms of leg-weakness, and during the following week, two individually-fed A pigs (gilt 2225 and hog 63) died. Post-mortem examination revealed no signs of the common infectious diseases, the primary cause of death being gastritis. All the A pigs at this stage were brought on to the B feeding treatment. This was considered desirable because, although a number of pigs on all the treatments had gone off their food, the A pigs seemed to be most affected. Moreover, meat meal A, with its very high-fat content, was the grade that would not ordinarily be fed in practice.

Table XVII. *Live-weight gains and meal consumption of individually-fed pigs over period 5 July to 18 October (15 weeks)*

Feeding treatment	No. and sex of pig	L.W. on 5 July lb.	L.W. on 18 October lb.	Total meal consumed lb.
Pen I (sow N 1)				
A	G 66	31½	149	364.50
B	G 61	33½	156	390.25
C	G 60	32	151½	393.75
C	H 68	28½	141	347.90
B	H 65	33½	147½	373.30
A	H 63	32½	147½	372.90
Pen II (sow C 2)				
B	G 78	45½	191½	487.15
C	G 77	45	160½	419.30
A	G 76	44	188½	482.30
C	H 83	45	177	466.90
A	H 82	45	184	458.40
B	H 84	35	167½	422.20
Pen III (sow 1413)				
C	G 2207	57	213	535.10
A	G 2206	55	201	504.45
B	G 2204	52½	192	490.25
B	H 2209	53½	208	525.30
C	H 2208	48½	177	481.55
A	H 2205	55	196	511.10
Pen IV (sow 1126)				
C	G 2240	45	176	455.90
A	G 2235	41½	167	407.00
B	G 2239	42½	179½	462.55
A	H 2238	38½	160½	414.75
B	H 2236	45½	189	485.10
C	H 2233	52½	192½	499.40
Pen V (sow 117)				
B	G 2228	42½	179½	449.55
A	G 2225	47½	183½	467.65
C	G 2224	46½	177	471.95
B	H 2226	47½	177	467.35
C	H 2222	49½	188½	494.05
A	H 2227	52½	189½	504.85

All the remaining affected animals made a good recovery during the week ending 22 September and resumed normal feeding. It should be kept in mind, however, that the A pigs were brought on to the medium-fat meat meal B treatment on 15 September, on which date the individually-fed A pigs averaged about 129 lb. live weight and the group-fed A pigs 109 lb. For the purpose of the statistical analysis, allowances were made in the case of the dead pigs by means of the "missing plot" technique. In addition to this, allowance had also to be made for gilt 2240 (individually-fed C pig), which proved to be a "waster" and weighed only 80 lb. at the end of the trial. Actual measurements, therefore, were carried out on 57 pigs. This naturally lowered the accuracy of the individual-feeding experiment, the degrees of freedom being reduced by three in the analysis of the variance.

Comments on Table XVII

Statistical analysis of the results for the individually-fed pigs revealed no significant differences between the mean live-weight increases of the pigs on the three feeding treatments over the 15 weeks of the comparison. The essential figures are:

Treatment	A	B	C	S.E.
Average L.W.I. (lb.)	132.35	135.60	130.45	2.96

Neither were there any significant differences in the total meal consumed by the pigs on the three different diets over the period of comparison:

Treatment	A	B	C	S.E.
Average meal consumption (lb.)	448.8	455.3	456.6	9.74

The results for the group-fed pigs broadly confirm the conclusion from the individual-feeding trial. The essential figures are:

Treatment	A	B	C	S.E.
Average L.W.I. over period (lb.)	116.15	126.30	113.05	6.71
Average meal consumption per pig (lb.)	412.1	433.5	417.2	—
Average lb. meal per lb. L.W.I.	3.55	3.43	3.69	—

The difference between the average live-weight gains of the pigs on the high-fat (A) and low-fat (C) meat meals is of a minor character, but it would appear that the pigs on the medium-fat meat meal B averaged a distinctly higher live-weight increase than the A and C pigs. Owing to the relatively high standard error of the means, however, the difference does not reach statistical significance.

In Table XVIII are summarized the results for both the individually-fed and group-fed pigs over the whole period of feeding up to 200 lb. live weight.

Table XVIII. *Results for whole period up to 200 lb. live weight (treatment averages)*

Treatment	Grade of meat meal	Individually-fed pigs				Group-fed pigs			
		Total lb. L.W.I.	No. of days on experiment	Mean lb. L.W.I. per day	Mean lb. meal per lb. L.W.I.	Total lb. L.W.I.	No. of days on experiment	Mean lb. L.W.I. per day	
A	High-fat	155.70	119.8	1.30	3.54	159.20	132.3	1.20	
B	Medium-fat	156.85	118.4	1.32	3.48	159.25	127.3	1.25	
C	Low-fat	155.05	121.0	1.28	3.63	158.35	135.3	1.17	
S.E.			2.64	0.023	0.05		6.3	0.05	

Comments on Table XVIII

The results in Table XVIII for the individually-fed pigs show no significant differences in the treatment averages for the number of days required to reach 200 lb. live weight, the mean rate of daily live-weight increase and the mean efficiency of food conversion over the period of feeding. There is, nevertheless, a suggestion that the pigs on the medium-fat meat meal made slightly more efficient gains than the A and C pigs. It will be noted that the group-fed pigs, despite their somewhat slower rate of growth, gave treatment averages showing slight differences very similar to those for the individually-fed pigs. Again, however, the differences did not reach statistical significance. The general conclusion may be drawn that, from the standpoint of rate of growth, there can be no objection to the use, in the amounts employed in this trial, of the medium-fat meat meal in the rations of bacon pigs.

POST-SLAUGHTER RESULTS (TRIAL II)

Table XIX. *Effect of feeding treatment on thickness of back fat and belly streak (treatment averages)*

Treatment	Grade of meat meal	Back fat*				Belly streak*			
		(a) mm.	(b) mm.	(c) mm.	Mean mm.	(a) mm.	(b) mm.	(c) mm.	Mean mm.
(1) Individually-fed pigs									
A	High-fat	52.5	26.9	38.0	39.1	26.6	36.9	44.6	36.0
B	Medium-fat	51.2	26.1	37.7	38.3	24.6	35.4	41.6	33.9
C	Low-fat	51.4	26.1	37.2	38.2	27.1	36.7	44.2	36.0
S.E.					0.70				0.56
(2) Group-fed pigs									
A	High-fat	48.2	24.1	34.6	35.6	28.1	36.4	43.0	35.8
B	Medium-fat	50.0	24.3	34.8	36.4	26.2	34.6	41.8	34.2
C	Low-fat	49.4	25.2	35.3	36.6	26.1	35.0	41.5	34.2
S.E.					1.03				0.93

* See footnotes to Table VII for positions of measurement.

Comments on Table XIX

The results are in harmony with those of Trial I in demonstrating that the use, in normal amounts, of meat meal A, containing 19.9% of fat, gave rise to no greater thickness of back fat or belly streak than was produced by the use of meat meal C, containing only 2% of fat. The only significant difference is that for the mean belly thickness of the carcasses from the individually-fed pigs. Although the mean values are identical for the pigs on the high-fat and low-fat meat meals, it would appear that the pigs on the medium-fat meat meal treatment had a significantly thinner belly streak. It is extremely improbable, however, that this difference is to be ascribed to a genuine effect of feeding treatment in view of the nature of the trend in this respect from treatment A to treatment C. The difference, moreover, is not shown by the group-fed pigs in the present trial, nor is it confirmed by the results of Trial I.

Table XX. *Effect of feeding treatment on size and leanness of typical rashers (treatment averages)*

Treatment	Grade of meat meal	"Warm" carcass weight lb.	Belly rasher*			Mid-back rasher*			Complete rasher*		
			Total area† sq. cm.	Area of		Total area† sq. cm.	Area of		Total area† sq. cm.	Area of	
				Lean sq. cm.	Fat sq. cm.		Lean sq. cm.	Fat sq. cm.		Lean sq. cm.	Fat sq. cm.
(1) Individually-fed pigs											
A	High-fat	159.3	89.68	26.90	59.92	123.21	39.54	81.24	212.89	66.44	141.16
B	Medium-fat	157.8	88.74	24.31	61.65	124.79	38.35	84.31	213.53	62.66	145.96
C	Low-fat	161.0	92.04	26.16	62.79	120.15	38.73	79.43	212.19	61.89	142.22
S.E.			1.84	1.12	2.15	1.93	1.28	2.21	2.97	1.64	3.65
(2) Group-fed pigs											
A	High-fat	158.9	85.55	27.67	54.95	117.34	40.28	74.20	202.89	67.95	129.15
B	Medium-fat	158.5	84.08	24.29	56.97	114.82	35.90	76.21	198.90	60.19	133.18
C	Low-fat	158.1	81.73	24.45	54.40	119.48	40.27	76.87	201.21	64.72	131.27
S.E.			2.29	1.31	2.67	3.01	1.50	3.60	4.85	2.93	5.97

* See first publication of this series for explanation of these terms (Woodman *et al.* 1936).

† Total area minus sum of areas of lean and fat equals area occupied by bone.

Comments on Table XX

The conclusions to be drawn from the figures in this table are in harmony with the findings of Trial I, namely, that there is no evidence of any consistent or significant effect of feeding treatment on the size and leanness of the typical rashers. The fortuitous character of the slight differences that may be discerned is emphasized by the finding that the treatment containing the high-fat meat meal gave rise to the leanest complete rasher (see Table XXI). The results lend no support to the belief that the use, in normal amounts, of grades of meat meal containing

a medium percentage of fat leads to the production of fatter bacon carcasses than are obtained when the extracted meat meal is used.

Table XXI. *Fat and lean as percentages of complete rasher (treatment averages)*

Treatment	Grade of meat meal	Individually-fed pigs		Group-fed pigs	
		Fat (%)	Lean (%)	Fat (%)	Lean (%)
A	High-fat	66.3	31.2	63.7	33.5
B	Medium-fat	68.3	29.3	67.0	30.3
C	Low-fat	67.0	30.6	65.2	32.2

Table XXII. *Influence of feeding treatment on "eye" muscle measurements (treatment averages)*

"Eye" muscle in mid-back rasher							
Space within line of connective tissue							
Treatment	Grade of meat meal	Total area sq. cm.	Area of		"Eye" muscle		Back fat opposite "eye" cm.
			Lean sq. cm.	Fat sq. cm.	Length cm.	Depth cm.	
(1) Individually-fed pigs							
A	High-fat	36.35	29.32	7.03	7.43	5.91	2.9
B	Medium-fat	35.05	28.64	6.41	7.43	5.51	3.1
C	Low-fat	35.67	29.09	6.58	7.83	5.53	3.0
S.E.		1.14	1.04	0.46	0.15	0.19	0.10
(2) Group-fed pigs							
A	High-fat	35.57	30.37	5.20	7.62	5.68	2.6
B	Medium-fat	32.57	27.14	5.43	7.35	5.36	2.8
C	Low-fat	35.21	29.17	6.04	7.32	5.82	2.8
S.E.		0.90	1.16	0.64	0.19	0.23	0.17

Table XXIII. *Influence of feeding treatment on certain post-slaughter measurements (treatment averages)**

Treatment	Grade of meat meal	Farm-fasted l.w. lb.	L.w. at factory lb.	"Warm" carcass percentage	Length cm.	Flares gm.	Sides as % of carcass weight
(1) Individually-fed pigs							
A	High-fat	199.8	194.4	82.00	74.2	1731	77.0
B	Medium-fat	199.1	193.3	81.65	74.0	1751	77.1
C	Low-fat	200.6	196.7	81.95	74.9	1810	77.1
S.E.				0.41	0.6	32.6	0.16
(2) Group-fed pigs							
A	High-fat	201.4	194.8	81.59	75.6	1502	77.3
B	Medium-fat	201.4	197.8	80.15	75.0	1536	76.8
C	Low-fat	200.7	195.0	81.09	76.0	1597	76.6
S.E.				0.50	0.58	106.9	0.22

* See footnotes to Table XII.

Comments on Table XXII

The results for the important "eye" muscle and the thickness of the back fat opposite the "eye" muscle lend further support to the conclusion that the carcasses of the pigs receiving the three meat meals were very similar in respect of their content of fat and lean. In this respect also, the results of the present trial are in agreement with those of Trial I.

Comments on Table XXIII

The results are in complete agreement with those of the first trial. Differences in the fat content of the meat meals produced no significant differences in respect of carcass percentage, length of pig, weight of flare fat and weight of sides expressed as a percentage of the carcass weight.

Table XXIV. *Influence of feeding treatment on iodine values of carcass fat (treatment averages)**

Treatment	Grade of meat meal	Iodine value of meat meal	Individually-fed pigs				Group-fed pigs			
			Back fat	Inner back fat	Belly fat	Flare fat	Back fat	Inner back fat	Belly fat	Flare fat
A	High-fat	48.5	66.30	58.27	62.96	52.50	67.04	61.28	64.00	53.39
B	Medium-fat	51.4	65.67	57.90	61.87	52.30	65.50	58.99	61.63	51.28
C	Low-fat	52.6	65.86	59.07	63.46	52.59	65.82	59.48	63.18	52.61
S.E.			0.48	0.55	0.62	0.57	0.73	0.95	0.70	0.56

* See footnotes to Table XIII.

Comments on Table XXIV

If the iodine value be taken as a reliable index of the firmness of the fat, then the results for the four samples of fat from the different regions of the carcass point to the conclusion that differences in the fat content of the meat meals had produced no corresponding significant differences in the consistency of the body fat. All the pigs yielded carcasses which, from the standpoint of the general appearance of the lean and fat, were of good marketable quality, a statement that was borne out by the results of actual tests of palatability. An analysis of the factory verdicts on the

Table XXV. *Analysis of factory opinion on quality of carcass fat*

			No. of carcasses with fat adjudicated as			
	Treatment	Grade of meat meal	Very firm	Firm	Medium firm	Slightly soft*
A	(18 pigs)	High-fat	4	12	1	1
B	(20 pigs)	Medium-fat	7	13	0	0
C	(19 pigs)	Low-fat	7	11	1	0

* See comments on Table XIV for explanation of this term.

quality of the fat in the cured sides of bacon is shown in Table XXV. The similarity in this respect between the carcasses from the treatments containing the marketable grades of meat meal (B and C) will be noted.

CONCLUSIONS

Two separate large-scale feeding trials have been carried out, at different periods of the year, to test whether the inclusion, in customary amounts in the rations of bacon pigs, of meat meals containing about 10% of fat gives rise to the production of fatter carcasses with a softer type of fat than are obtained by the use of extracted meat meals containing only 2-3% of fat. The main question at issue was whether it is necessary to submit meat meals to extraction with petroleum benzine at 200° F. in order to obtain a product suitable for including in the rations of bacon pigs, particularly in view of the expense of the extraction and the fact that the process may cause some depression of the digestibility of the meat meal. In order that the effect of the meat meal fat on carcass quality might be tested under more stringent conditions than are likely to be encountered in feeding practice, comparative tests were also made with meat meals containing as much as 17-20% of fat.

The experimental rations contained 10% of the meat meals up to the stage when the pigs had reached 150 lb. live weight, and the amount was reduced to 5% from 150 lb. to slaughter at about 200 lb. live weight. The food supply of the pigs was scaled so as to reach a maximum of 7 lb. per head per day at 200 lb. live weight. Large-White pigs were used in the trials, and both the individual-feeding and group-feeding techniques were employed.

Under the conditions of the present trials, the feeding treatments containing the three different meat meals gave rise to no significant differences in the rate of live-weight increase and the efficiency of food conversion. Nor were there any significant differences between the pigs receiving the different meat meals in respect of carcass fatness, as judged by the thickness of the back fat and belly streak, the size and leanness of certain typical rashers and of the "eye" muscle, the weight of flare fat and the weight of the fillets. No significant differences were found in the figures for length, carcass percentage and the weights of the sides of bacon expressed as a percentage of the carcass weight.

The bacon carcasses as a whole, irrespective of feeding treatment, were judged by the factory expert to be of very satisfactory marketable quality. There was evidence of some slight improvement in the firmness of

the carcass fat on passing from treatment A, containing the meat meal with 17-20% of fat, to treatments B and C, in which were included respectively the meat meals containing 9-10 and 2-3% of fat. Such differences, however, were of no significance from the curer's standpoint. The differences in this respect between the carcasses from the pigs on treatments B and C, which contained the marketable grades of meat meal, were of an entirely insignificant character. The judgment of the factory expert was fully confirmed by determinations of the iodine values of samples of body fat taken from four different regions of the carcass.

The results of this investigation give no support to the prejudice against the use of meat meals containing about 10% of fat on the grounds that meat meals of this fat content lead to the production of fatter carcasses and to an undesirable softening of the body fat. The findings discussed in this paper point clearly to the conclusion that meat meals of this composition, when included in the amounts employed in this investigation, give as good results as may be obtained from the use of extracted meat meals of very low fat content.

In conclusion, the authors desire to express their thanks to Messrs W. Weddel and Co., Ltd. for supplying the grades of meat meal used in this investigation. Grateful acknowledgements are also made to Mr J. Andreasen, of the St Edmundsbury Co-operative Bacon Factory, for granting facilities for carrying out the factory part of the trials. The writers also take this opportunity of stating their indebtedness to Dr J. Wishart for taking charge of the statistical analysis of the results and to Dr E. H. Callow and his staff for help in the making of the factory measurements. Thanks are expressed to Mr E. A. Porter, who had charge of the pigs throughout the feeding trial.

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THE INFLUENCE OF MANURIAL TREATMENT ON THE CAROTENE CONTENT OF POOR PASTURE GRASS, AND ON THE RELATIONSHIP OF THIS CONSTITUENT TO THE ASH AND ORGANIC FRACTIONS

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THE value of carotene in the animal diet is now too well known to need any comment, and the importance of grass as the chief source of carotene is clearly shown by the fact that over 70% of the enclosed agricultural land in England and Wales is devoted to the cultivation of this crop. Relatively little study has been made of the conditions which control the formation of carotene in plants or of the relation between carotene and other plant constituents; such information as is available relates almost entirely to crops other than grass, and has been derived largely from the results of experiments in pots.

During recent years the author has been engaged in a field study of some of the chief factors influencing the carotene content of grass, viz. maturity, botanical composition of the herbage, season and manurial treatment. An examination of the influence of maturity (Thomas & Moon, 1938; Moon, 1939*b*) has shown that carotene content does not vary substantially during a growth period of 4 weeks, but declines very markedly at the commencement of the flowering period, whilst an investigation of several species of pasture plants (Moon, 1938, 1939*c*) has shown some considerable differences in the carotene contents of grasses, clovers and weeds. Information on seasonal variations in the carotene content of repeatedly cut grass has been obtained from the manurial investigation of Thomas & Moon (1938); similar information for non-intensive grass has also been obtained during the growing season of 1938 and during the winter of 1938-9, but this data has not yet been fully examined.

In the previous manurial experiment (Thomas & Moon, 1938) duplicate plots were used, arranged so as to compensate for any fertility drift in the direction of the major axis of the experimental area, and four treatments were examined, viz. no manure, sulphate of ammonia,

sulphate of iron and carbonate of lime; only the sulphate of ammonia was found to produce an increased carotene content. During the following year (1938) a similar, but more comprehensive experiment was carried out, six manurial treatments being investigated in six-fold replication, using a random block layout. This experiment was laid down on a much poorer type of grassland than the previous one, and in addition to providing information on manurial differences and seasonal variations, it was hoped to obtain some indication of the relationship between carotene and the major plant constituents. Although several significant correlations were obtained (Moon, 1939*b*) with grass varying principally in degree of maturity, no similar information was available for young grass of constant age, grown under various manurial treatments.

EXPERIMENTAL

The experiment to be described was laid down at the Northumberland County Experimental Station, Cockle Park, on a portion of the Glents pasture which had received no manure for a period of 42 years, except that left by the grazing stock. The soil is a fairly heavy loam, with the following analysis:

	% of air-dry sample		% of air-dry sample
Coarse sand	11.95	HCl-soluble P_2O_5	0.110
Fine sand	33.10	HCl-soluble K_2O	0.130
Silt	15.58	Available P_2O_5	0.015
Clay	25.80	Available K_2O	0.018
Moisture	3.22		
Carbonates	Nil		
Loss by solution	2.11		
Difference	8.24	pH	5.36
	100.00		

For the purpose of this experiment a total area of $47\frac{1}{2}$ ft. \times 32 ft. was divided into six blocks, each of which was further subdivided into six plots of dimensions 2 ft. \times 15 ft., there being $\frac{1}{2}$ ft. margins between plots. The allocation of treatments was randomized separately for each block in the ordinary way, and the composition and rates of application of the five different fertilizers were as shown in Table I. Owing to the poor condition of the pasture, it was considered advisable to apply these very heavy dressings of artificial fertilizers, in order to ensure the detection of any manurial effects. The marked influence of these dressings on the reaction of the soil and on the amounts of citric-soluble constituents is clearly shown by the analyses of soil samples taken after the conclusion

Table I. *Manurial treatments*

Manure	Dry matter %	Analysis of air-dry sample	Initial dressing (24 Mar.)		Subsequent monthly dressing	
			cwt. per acre	g. per plot	cwt. per acre	g. per plot
Sulphate of potash	99.21	50.73 % K_2O	2	83.4	1	41.7
Carbonate of lime	96.63	85.53 % $CaCO_3$	80	3336.0	Nil	Nil
Superphosphate	93.95	{ 18.75 % total P_2O_5 18.27 % sol. P_2O_5	6	250.2	4	166.8
Nitrate of soda	99.87	16.35 % nitrate nitrogen	(1 + $\frac{1}{16}$)	54.7	(1 + $\frac{1}{16}$)	54.7
Sulphate of ammonia	99.92	21.02 % ammonia nitrogen	1	41.7	1	41.7

Table II. *Analyses of soil after conclusion of experiment*

Manurial treatment	pH	Available P_2O_5	Available K_2O
		%	%
None	5.60	0.017	0.015
Sulphate of potash	5.45	0.014	0.035
Carbonate of lime	7.21	0.010	0.015
Superphosphate	5.22	0.039	0.014
Nitrate of soda	6.12	0.020	0.017
Sulphate of ammonia	5.19	0.015	0.013

of the experiment (cf. Table II). The amount of carbonate of lime applied was in excess of the estimated requirement, and increased the soil pH from 5.36 to 7.21. Nitrate of soda, supplying the exchangeable base sodium, also had a favourable influence on soil reaction, but the repeated applications of sulphate of ammonia, on the other hand, resulted in an increased acidity. As was to be expected, the superphosphate plots showed marked increases in available phosphate, and the sulphate of potash plots, in available potash.

The rates of application of the two nitrogenous manures were calculated to supply equal amounts of nitrogen, and from the analyses in Table I it appears that whereas the sulphate of ammonia supplied 8.77 g. nitrogen per plot, the nitrate of soda contributed slightly more (8.94 g. per plot).

SAMPLING AND ANALYSIS

The whole experimental area was cleared on 23 and 24 March, and the initial manurial dressings shown in Table I were applied on the latter date. Thereafter the plots were cut regularly each month, with an ordinary 12 in. garden mower, the further manurial dressings (cf. Table I) being applied immediately after cutting. On all occasions the total yield of each plot was placed in an airtight tin and immediately transferred to

the laboratory, where it was weighed and dried at 100° C. for 24 hr. For carotene determinations 5 g. samples were removed prior to drying, and these were preserved in alcohol, as described below. Determinations of the ash, silica and major organic constituents in the dried samples were carried out by the usual analytical methods, and corrections for soil contamination were made on the basis of silica content, assuming the figure of 2.0% for clean pasture grass.

Preservation of samples and determination of carotene

As it was not possible to determine carotene immediately in the large number of samples involved in this experiment, some means of preservation was essential. A preliminary investigation (Moon, 1938) had shown low-temperature drying to be useless for this purpose, and experiments with drying in nitrogen were equally unsuccessful. The following method of storage, which was finally adopted, proved to be very satisfactory and resulted in no loss of carotene. 5 g. of the chopped fresh sample were weighed out and transferred to a 100 c.c. glass jar, provided with metal screw cap and cork disk to provide an airtight seal; 50 c.c. of ethyl alcohol were then added, and the jar placed in a vacuum desiccator. After evacuation the pressure was restored to normal with nitrogen, which was obtained from a cylinder and purified from traces of oxygen by passing through a series of pyrogallol washers. The desiccator was then evacuated for a second time and again filled with nitrogen, after which it was opened and the jar capped immediately. Treated in this way and stored in the dark, samples may be kept for some considerable time without loss of carotene; in this investigation, however, all analyses were completed within a week of sampling.

For carotene determination the contents of the jar were transferred to a large glass funnel containing a small porcelain disk covered with filter paper. The excess alcohol was drawn off by suction and the grass residue pressed dry with a spatula, transferred to an Erlenmeyer flask, and saponified in the usual way (Moon, 1939*a*). The alcohol filtered off from the "preserved" grass was transferred back to the storage jar and a little solid potassium hydroxide added. After saponification, the grass residue was extracted with only 50 c.c. alcohol, the 50 c.c. used for the initial preservation being then added from the jar. The process of determining carotene was completed exactly as described by Moon (1939*a*).

BOTANICAL NOTES

It is well known that marked changes can be brought about in the botanical composition of pasture grass by repeated mowing, and in order to obtain some information on the changes occurring as a result of the different manurial treatments employed in this experiment, botanical analyses were carried out by the percentage area method at the beginning of September. An analysis was also made of the untreated herbage close to the experimental area, which had not been subjected to repeated defoliation. The results obtained are summarized in Table III.

Table III. *Summary of botanical analyses*

Species	Un-treated %	Manurial treatment					
		None %	Sulphate of potash %	Carbon- ate of lime %	Super- phos- phate %	Nitrate of soda %	Sulphate of ammonia %
Fescue and Bent (<i>Festuca</i> and <i>Agrostis</i> spp.)	50.5	45.2	43.3	42.7	43.6	57.8	54.3
Yorkshire fog (<i>Holcus lanatus</i>)	24.9	15.6	16.1	14.6	20.4	15.8	23.2
Sweet vernal (<i>An- thoxanthum odoratum</i>)	7.2	8.8	9.8	10.4	9.9	5.7	10.5
Crested dogstail (<i>Cynosurus cristatus</i>)	1.6	4.8	4.3	3.7	3.7	8.1	4.7
Other grasses	1.1	3.8	6.6	1.5	1.9	4.3	1.9
Wild white clover (<i>Trifolium repens</i>)	8.1	7.8	8.4	15.2	9.5	1.0	0.8
Trefoil (<i>Lotus corniculatus</i>)	0.7	4.0	3.8	6.0	3.7	1.3	0.6
Plantain (<i>Plantago sp.</i>)	2.5	5.2	5.5	2.7	4.8	5.3	1.4
Other weeds	3.4	4.8	2.2	3.2	2.5	0.7	2.6

The increase in fescue and bent and the decrease in wild white clover resulting from nitrogenous manuring, is very noticeable. Wild white clover increased considerably on the limed plots, and trefoil on all plots except those treated with nitrate of soda. The increases in plantain shown under most treatments were probably due to an increased size of growth, resulting from the reduced competition of the repeatedly defoliated grasses.

METEOROLOGICAL DATA

Rainfall, sunshine and temperature data for the period March-September 1938, together with the mean rainfall and sunshine figures for the corresponding months in the preceding 20 years, are given in

Table IV. *Meteorological data*

Month	Rainfall in.	Average rainfall for 20 years 1918-37 in.	Sunshine hr.	Average sunshine for 20 years 1918-37 hr.	Temperatures		
					Mean grass min. °F.	Mean screen max. °F.	Mean screen min. °F.
March	0.42	1.87	105	105	38.4	53.9	41.8
April	0.15	2.14	134	133	35.1	51.9	37.6
May	3.50	2.22	156	168	39.2	55.5	40.4
June	2.66	1.75	181	183	45.0	61.3	47.0
July	2.67	2.80	118	164	46.7	62.9	49.0
August	4.74	3.00	141	154	48.7	63.5	50.0
September	1.97	2.53	113	129	45.0	61.6	46.7

Table IV. The total rainfall during March and April was exceptionally low, being less than 25% of average during the former month and less than 8% of the average during April. In the latter half of May and in June and August, however, the weather was quite different, the total precipitation in each of these months exceeding the means for the corresponding months during the period 1918-37, by more than 50%. Hours of bright sunshine were more or less normal in all months except July, when the figure recorded in 1938 was more than 25% less than the average for that month. Temperatures were rather low during April and many cold nights were also noted during March and early May, although higher maximum temperatures were experienced in these two months; during the remainder of the experimental period the weather was quite warm, temperatures being about normal.

RESULTS

I. *Carotene content, yields of dry matter and yields of carotene*

Influence of manurial treatment.

Space does not permit the full tabulation of results, but the mean carotene contents and yields of carotene and dry matter are given below, together with the differences necessary for significance. It will be seen

Table V. *Treatment means*

	No manure	Sulphate of potash	Carbon- ate of lime	Super- phos- phate	Nitrate of soda	Sulphate of ammonia	Signi- ficant differ- ence
Carotene (mg. per 100 g. dry matter)	40.56	43.09	40.97	41.91	51.19	52.61	1.57
Yield of dry matter (g. per plot)	56.92	65.35	65.71	76.63	94.67	114.84	6.49
Yield of carotene (mg. per plot)	24.30	29.69	28.78	34.41	51.68	65.08	3.78

that the two nitrogenous manures have produced similar increases in carotene content, the mean figures for these treatments being about 28% greater than for the control (unmanured) plots. The only other manurial treatment which had a significant effect on carotene content was sulphate of potash, which produced an increase of 6.2%. Carbonate of lime, applied in an amount which was sufficient to raise the soil pH to 7.2, led to no increase, a result similar to that obtained in the previous investigation (Thomas & Moon, 1938). Superphosphate was also without significant effect on carotene content.

The increases obtained with sulphate of ammonia and nitrate of soda were fully expected in view of the results obtained with sulphate of ammonia in 1937, and of the investigations which have been carried out on other plants by Guthrie (1929), Virtanen *et. al.* (1933), Ijdo (1936) and other workers. Although Virtanen and his collaborators have stated that, for the production of carotene, nitrates are superior to ammonium salts, it has already been indicated (Thomas & Moon, 1938) that such a conclusion is difficult to substantiate from their results with wheat. At optimum pH (6.5) the carotene contents obtained by Virtanen with the three manures, ammonium sulphate, potassium nitrate and ammonium nitrate, each supplying the same quantity of nitrogen, were 0.083, 0.113 and 0.181 mg. per g. respectively; thus, although the two manures containing nitrate nitrogen produced higher carotene contents than the sulphate of ammonia, there was no evidence of any superiority of potassium nitrate over ammonium nitrate. Virtanen has also assumed that nitrate nitrogen is more available than ammoniacal nitrogen, and has therefore concluded that carotene content is directly related to the facility with which the plant can utilize a given nitrogen supply. Although it was believed for a long time that nitrogen was assimilated by plants only in the form of nitrate, Maximov (1938) states that experiments carried out with sterile cultures have shown this concept to be false, and that "under conditions favourable for the growth of plants ammonium salts are assimilated just as well as nitrates". Although the dressings of nitrate of soda applied in this investigation provided slightly more nitrogen than the sulphate of ammonia, no significant difference was observed in the influences of these two manures on carotene content. It is also interesting to note that the increased carotene content produced by the two nitrogenous treatments on a pasture consisting very largely of bent and fescue, is quite equal to that obtained in the previous investigation on a sward composed very largely of Yorkshire fog.

There is relatively little reference in the literature to the influence of

potassium salts on carotene content. Ijdo (1936), however, claims that there is a close physiological interrelation between nitrogen and potassium, and that, in respect of their influences on carotene content, potassium deficiency has the effect of nitrogen excess, whilst potassium excess acts like a nitrogen deficiency. This worker used spinach plants for his experiments, and found that increasing the potassium content of the soil reduced the carotene content, except when nitrogen was also applied. According to the early work of Ville (1889), however, potassium is most essential for carotene production in such plants as potatoes and vines. This work does not appear to have been confirmed, and in the case of potatoes some contradictory evidence has since been presented; thus, according to Schertz (1929), the application of potash has an adverse influence on the formation of carotene in potatoes. In view of the somewhat contradictory evidence regarding the influence of potassium, the significant effect on the carotene content of grass in this experiment is of considerable interest.

Ijdo (1936) has shown that calcium salts and phosphates have little effect on the carotene content of spinach, and similar results have been obtained in the present experiment with grass. Although the mean carotene content for the superphosphate plots was greater than for the unmanured plots, the difference could not be considered significant. Reaction is known to exert a predominant influence on the nitrification in pasture soils (Thomas & Elliott, 1932) and an increased carotene content might, therefore, have been expected from the application of carbonate of lime. No such result was obtained in the previous manurial investigation, although it should be noted that the lime was not applied until May and, therefore, could not be expected to have exerted its maximum effect before the conclusion of the experiment in September. In the present experiment the dressings of lime were applied in March, but still no beneficial effect on carotene content was observed. It has already been shown that the lime applied was sufficient to raise the soil pH from 5.36 to 7.21, and to produce an increase of almost 100% in the wild white clover content of the sward; these changes would seem to indicate that the lime had at least commenced to exert an effect. Furthermore, the enhanced clover content might itself have been expected to result in an increase of soil nitrogen, since Virtanen (1938) has shown that considerable quantities of nitrogenous products are excreted into the soil during the early stages of intranodular nitrogen fixation.

The figures in Table V show an increased dry-matter production under all five manurial treatments, this being as much as 100% with

sulphate of ammonia and over 66% in the case of nitrate of soda. Sulphate of potash and carbonate of lime produced increases of over 12%, whilst the corresponding figure for superphosphate was almost 35%.

As a result of the universal increase in dry-matter production the yields of carotene produced by all five fertilizers were significantly greater than those of the control plots. These increases in yield were particularly marked with sulphate of ammonia and nitrate of soda, being well over 100% in each case, whilst even with sulphate of potash and carbonate of lime they amounted to 20%. The superphosphate plots occupied an intermediate position, with a carotene production more than 40% above that of the control treatment.

Seasonal variation.

The occasion means given in Table VI show the carotene contents to have been very low in April and May; these results were not unexpected, as there was a very pronounced drought at that period (cf. Table IV), and the early samples were not entirely free from dead grass, remaining from the previous season's growth. A highly significant increase of 19% occurred in June and, although no further change was observed in

Table VI. *Occasion means*

	20 April	16 May	13 June	11 July	8 Aug.	5 Sept.	5 Oct.	Significant difference
Carotene (mg. per 100 g. dry matter)	27.36	34.98	43.26	42.49	52.07	49.96	65.25	1.70
Yield of dry matter (g. per plot)	20.74	17.01	101.01	124.39	134.91	90.30	64.78	7.01
Yield of carotene (mg. per plot)	5.72	6.09	45.25	54.95	72.05	45.98	42.89	4.08

July, there were very marked and highly significant increases in the autumn months, the mean carotene content in October being 65.25 mg. per 100 g. dry matter. It will be noted (cf. Table IV) that temperatures during August were higher than in either July or September and, although the hours of sunshine were below average and rainfall was well above average in this month, a certain amount of "burn" was evident in the grass sampled on 5 September. This seems most likely to have resulted from the very cold nights immediately preceding the September sampling; although no frosts were recorded, the mean grass minimum temperature for the period 30 August-3 September was only 37.75° F. As a result of the "scorching" noted on this occasion, the mean carotene content was significantly lower than in August and October.

The very marked rise in carotene content, which was observed during the autumn months, was similar to that occurring in the previous investigation, when the final value obtained on 30 September was 66.1 mg. per 100 g. dry matter. There seems to be little doubt of the universal increase in carotene content which occurs during the late summer and autumn, although such increases are rather difficult to explain on theoretical grounds; if, as Virtanen and his co-workers (1933) suggest, carotene is associated with growth, then high carotene contents would be expected in the spring, but not during late summer and autumn. High carotene contents have been observed in clean pasture plants examined in the early spring (Moon, 1939c), and the low figures obtained in this investigation during March and April have already been accounted for on the basis of weather conditions and contamination of the samples. Further, with grass of the type examined in this investigation, growth does not commence very early in the year and, under the conditions of 1938, did not take place to any appreciable extent before the latter half of May.

A good indication of the growth taking place during the season is given by the mean dry-matter yield for each month. The extremely low figures obtained in April and May, which correspond to a production of about 64 lb. dry matter per acre, are outstanding. During June, July and August, however, yields increased very considerably, the figure obtained in August being equivalent to 432 lb. dry matter per acre. Lower dry-matter productions were obtained in September and October, when the growing season was drawing to a close. On all occasions considerably less dry matter was produced by this poor herbage than by the better type of grass examined at corresponding periods in 1937 (Thomas & Moon, 1938).

Yields of carotene followed those of dry matter fairly closely, although the very high carotene content in October did much to offset the low dry-matter yield on this occasion. Consequently the yields of carotene were very low in April and May, much higher and rather similar in June, September and October, and greatest in August, when the maximum yield of grass was produced.

Treatments \times occasions interaction.

The influence of season on the individual manurial treatment effects is shown in Table VII. The similarity in the behaviour of nitrate of soda and sulphate of ammonia throughout the whole season is shown by the fact that on no occasion did the mean carotene contents obtained under

these two treatments differ significantly. Although the increases in carotene content produced by nitrate of soda in April and May were very small and barely significant, sulphate of ammonia, which also produced only a very small effect on the first application did, however, produce a decidedly significant increase in May. This difference cannot easily be explained, although the small and rather erratic results obtained in the early months were to be expected in view of the dry weather prevailing.

Table VII. *Interaction: treatments and occasions*

	20 April	16 May	13 June	11 July	8 Aug.	5 Sept.	3 Oct.
mg. carotene per 100 g. dry matter (significant difference = 4.64)							
No manure	24.47	32.74	38.20	36.96	46.06	44.51	60.98
Sulphate of potash	25.98	35.09	39.71	40.52	49.98	45.90	64.48
Carbonate of lime	25.59	34.02	37.02	36.91	49.49	45.16	58.58
Superphosphate	24.86	31.49	43.73	40.94	44.48	47.53	60.33
Nitrate of soda	31.51	36.34	50.69	48.34	59.24	56.35	75.83
Sulphate of ammonia	31.75	40.21	50.21	51.25	63.20	60.33	71.32
g. dry matter per plot (significant difference = 19.12)							
No manure	17.72	17.41	66.61	87.27	94.16	67.64	47.68
Sulphate of potash	22.50	20.04	85.13	95.15	105.73	74.67	54.24
Carbonate of lime	18.71	16.63	80.65	92.79	103.13	84.27	63.81
Superphosphate	16.78	14.44	89.08	122.21	149.65	88.61	55.62
Nitrate of soda	23.79	14.36	117.67	166.21	161.75	107.59	71.32
Sulphate of ammonia	24.98	19.17	166.93	182.71	195.01	119.05	96.00
mg. carotene per plot (significant difference = 11.14)							
No manure	4.29	5.80	25.51	32.27	43.04	30.19	29.03
Sulphate of potash	5.73	6.94	33.97	38.72	53.21	34.25	35.01
Carbonate of lime	4.84	5.63	29.83	34.83	50.78	38.16	37.40
Superphosphate	4.22	4.70	39.58	50.50	66.61	41.72	33.56
Nitrate of soda	7.47	5.38	59.52	79.89	95.59	60.09	53.85
Sulphate of ammonia	7.77	8.10	83.10	93.48	123.11	71.49	68.52

During the remainder of the experiment the increases in carotene content produced by nitrate of soda showed relatively little variation from month to month, although sulphate of ammonia was not so consistent in its results. The percentage increases of carotene content over the means for control plots are shown below and it will be noted that in both cases

Percentage increases in carotene content

	May	June	July	Aug.	Sept.	Oct.
Nitrate of soda	(not sig.)	32.7	30.8	28.6	26.6	24.4
Sulphate of ammonia	22.8	31.4	38.7	37.2	35.5	17.0

there is evidence of a declining effect as the season advances; although this might be expected to occur with repeated applications of manure by reason of the "law of diminishing returns", it is also possible that the June and July effects were enhanced by the previous dressings, which could scarcely have been utilized during the period of drought.

Although the mean carotene contents shown by Table VII for the plots manured with sulphate of potash are consistently greater than those of the unmanured plots, on no single occasion was this difference significant. There can be no doubt as to the significance of the influence of sulphate of potash shown in Table V, and the insignificant effects shown in Table VII are almost certainly the result of the reduced accuracy of these comparisons, shown by the greater differences necessary for significance.

As was to be expected, the effect of lime on carotene content was not significant on any single occasion. In the case of superphosphate, however, a carotene content significantly greater than that of the control plots was observed on 13 June, although no effect had been shown by the mean figure for the whole season. No significant increase had been expected in April and May as several of the superphosphate plots showed an appreciable amount of scorching at that period. Whilst it is possible that superphosphate may have increased the carotene content in April and May under more favourable weather conditions, in this experiment an increase was only obtained in mid-season, and there was no evidence of any similar effect in late summer and autumn (August–October).

The effects of nitrate of soda and sulphate of ammonia on dry-matter production were significant in all months except April and May and, as shown below, sulphate of ammonia produced the greater increases. It has been shown previously that sulphate of potash and carbonate of

Percentage increases in dry-matter yields

	June	July	Aug.	Sept.	Oct.
Nitrate of soda	76.7	90.5	71.8	59.1	49.6
Sulphate of ammonia	150.6	109.4	107.1	76.0	101.3

lime increased the mean seasonal dry matter yields by about 12%; the increases shown in Table VII could not be considered significant owing to the greater error associated with these comparisons. Superphosphate, which gave a mean yield of dry matter almost 35% greater than the control treatment, produced significant increases during the period June–September, but not in April, May or October. The lack of response during April and May should need no explanation and the declining growth at the end of the season would easily account for the October result; the growth-stimulating power of superphosphate at this period is very small in comparison with that of the nitrogenous manures.

Yields of carotene were very similar to those of dry matter, there being no significant increases for the sulphate of potash or carbonate of

lime treatments, but very significant increases for nitrate of soda and sulphate of ammonia in all months but April and May. Superphosphate produced yields of carotene significantly greater than those of the control plots, in all months but April, May and October. Seasonal variations in carotene production were similar under all treatments, the maximum occurring in August.

II. *Ash and organic constituents*

The present investigation was not designed primarily to examine the influence of the various treatments on the amounts of ash and organic constituents in the dry matter of the grass produced, but these were determined in order to provide some information on their relationship to carotene content, which is discussed in Section III. Analyses of variance were, however, carried out with the data for these fractions, and it may be of some interest to discuss briefly the results obtained, which are summarized in Tables VIII, IX and X.

Influence of manurial treatment.

Under all three non-nitrogenous treatments, viz. sulphate of potash, carbonate of lime and superphosphate, the ash content of the grass was significantly greater than that of the unmanured herbage. It is well

Table VIII. *Treatment means (% of dry matter)*

	No manure	Sulphate of potash	Carbon- ate of lime	Super- phos- phate	Nitrate of soda	Sulphate of ammonia	Significant difference
Ash	8.42	9.02	8.98	9.77	7.84	8.62	0.25
Crude protein	18.81	18.96	19.05	19.71	22.24	22.79	0.38
Ether extract	3.54	3.53	3.49	3.74	3.59	3.77	0.12
N-free extract	49.27	48.26	48.67	46.58	46.38	45.02	0.61
Fibre	19.96	20.25	19.81	20.20	19.96	19.80	0.31

known that mineral fertilizers increase the ash constituents of pasture grass, especially where the supply of available minerals in the soil is not particularly great, and the results obtained in this investigation were in accordance with expectations. No significant effect was observed in the case of sulphate of ammonia, although nitrate of soda significantly decreased the percentage of total ash.

Increases in protein content of 18.2 and 21.2% were produced by nitrate of soda and sulphate of ammonia respectively, whilst the application of superphosphate produced the significant increase of 4.8%. Sulphate of potash and carbonate of lime had no influence on nitrogen content.

Ether extract was only affected by two of the manures investigated, viz. superphosphate and sulphate of ammonia, both of which produced significant increases. Nitrogen-free extract, on the other hand, was significantly lowered with all manures except carbonate of lime; since this fraction is a "difference" figure, the lowered content is very probably the result of an increased content of the other organic constituents. None of the five manurial treatments produced any significant effect on the fibre content of the herbage.

Seasonal variation.

The change in ash content between April and May cannot be considered of any importance, since at this period the figures would be affected by

Table IX. *Occasional means (% of dry matter)*

	20 April	16 May	13 June	11 July	8 Aug.	5 Sept.	3 Oct.	Significant difference
Ash	8.56	8.00	8.51	8.63	9.66	8.87	9.20	0.27
Crude protein	20.01	21.05	18.37	18.17	20.04	20.36	23.82	0.41
Ether extract	2.80	3.36	3.53	3.50	4.40	3.61	4.07	0.13
N-free extract	50.97	47.76	49.14	48.24	44.43	47.18	43.91	0.66
Fibre	17.65	19.85	20.44	21.47	21.57	19.98	19.00	0.33

dead material remaining from the previous season's growth. The tendency for increasing ash contents during the latter part of the season, which has previously been noted by Cruickshank (1926), is evident in the results obtained in this investigation. Crude protein showed the normal seasonal variation, the minimum value being in July and the maximum in October, whilst ether extract increased during the spring and early summer to a maximum in August, and decreased slightly during the autumn. Nitrogen-free extract showed a somewhat erratic variation, whilst fibre increased regularly from April to August, and then showed the normal decrease in September and October.

Treatments \times occasions interaction.

The data in Table X illustrate the interaction between treatments and occasions for ash, crude protein, ether extract and fibre: the interaction for nitrogen-free extract was shown by the z test to be not significant.

The influence of the three mineral manures on ash content has already been mentioned, and it is seen from Table X that the effect of superphosphate was significant on all occasions. The increases produced by the other two were not so great and were only significant in April and May in the case of carbonate of lime, and in April and June in the case

of sulphate of potash. Neither of the two nitrogenous manures had any influence on ash content on any occasion, and the seasonal variations of this constituent were similar under all manurial treatments.

The protein increases obtained with nitrate of soda and sulphate of ammonia were significant on all occasions, although the increases obtained with superphosphate only exceeded the values necessary for significance in May and September. Neither sulphate of potash nor carbonate of lime had any significant influence on the mean protein content for the season (cf. Table VIII), but the latter did produce a significant increase in September; the consistently superior protein content produced by this treatment on all occasions but the first, suggests that carbonate of lime may have produced a slight increase, although the present experiment could not show it to be significant. Normal seasonal variation occurred under all treatments.

Table X. *Interaction: treatment and occasions*

	20 April	16 May	13 June	11 July	8 Aug.	5 Sept.	3 Oct.
	% ash (significant difference = 0.73)						
No manure	7.55	7.43	7.90	8.55	9.79	8.71	9.06
Sulphate of potash	8.98	7.98	8.78	8.79	9.87	9.32	9.40
Carbonate of lime	9.98	8.98	8.18	8.30	9.34	8.84	9.24
Superphosphate	9.58	8.79	9.87	9.57	10.81	9.77	10.01
Nitrate of soda	7.49	6.98	7.86	7.99	8.73	7.76	8.06
Sulphate of ammonia	7.80	7.82	8.48	8.58	9.40	8.83	9.45
	% crude protein (significant difference = 1.11)						
No manure	19.31	18.92	16.98	16.81	19.35	18.11	22.23
Sulphate of potash	18.72	19.14	16.90	17.52	19.05	18.98	22.40
Carbonate of lime	17.66	19.12	17.00	17.12	19.88	19.45	23.11
Superphosphate	19.80	20.68	17.58	17.62	19.52	19.76	23.02
Nitrate of soda	22.31	24.20	20.80	19.49	20.96	22.28	25.65
Sulphate of ammonia	22.29	24.22	20.97	20.45	21.50	23.60	26.52
	% ether extract (significant difference = 0.35)						
No manure	2.77	3.56	3.41	3.33	4.16	3.38	4.16
Sulphate of potash	3.00	3.23	3.49	3.44	4.24	3.44	3.89
Carbonate of lime	2.33	3.32	3.35	3.39	4.37	3.58	4.13
Superphosphate	2.87	3.45	3.73	3.56	4.49	3.87	4.24
Nitrate of soda	2.83	3.04	3.42	3.47	4.73	3.70	3.94
Sulphate of ammonia	3.02	3.58	3.81	3.81	4.39	3.70	4.05
	% fibre (significant difference = 0.91)						
No manure	17.96	20.02	20.80	20.64	20.70	20.03	19.56
Sulphate of potash	17.98	20.10	20.97	21.27	21.58	20.35	19.48
Carbonate of lime	16.43	20.14	20.35	21.73	21.33	19.90	18.78
Superphosphate	18.48	19.91	20.84	21.68	21.53	20.02	18.93
Nitrate of soda	18.03	19.72	19.38	21.62	22.06	20.03	18.86
Sulphate of ammonia	17.03	19.21	20.32	21.86	22.24	19.53	18.41

It has already been shown that only superphosphate and sulphate of ammonia produced increases in the mean ether extract content of the

grass; owing to the reduced accuracy of the comparisons in Table X the majority of the increases obtained with these manures on single sampling occasions were not significant. It should be noted, however, that nitrate of soda, which gave no significant increase over the whole season, did produce a significant increase in August, the occasion when maximum values were obtained for ether extractives.

Although no manurial treatment differences were observed in respect of fibre content for the whole season's analyses, several significant differences are evident in the data presented in Table X for the interaction comparisons; outstanding amongst these are the significantly increased fibre contents obtained in July with carbonate of lime, superphosphate, nitrate of soda and sulphate of ammonia, and also in August with the two nitrogenous manures. It will be noted that the control plots, and also those receiving sulphate of potash, showed relatively slight variation in fibre content between May and October; under the other four treatments, however, fibre increased regularly from April until July or August, and declined somewhat in September and October, a variation which is quite normal under conditions of repeated cutting. It will be observed that the manurial treatment effects referred to above occurred at the period of maximum fibre content, i.e. in July and August; with the exception of this period the herbage of the control plots had a higher fibre content than the other plots, this difference being significant for nitrate of soda in June and for sulphate of ammonia in October.

III. *Correlation of carotene with ash and organic constituents*

The relationship between carotene content and the percentages of ash and organic constituents is shown by the correlation coefficients in Table XI, the figures in brackets being the corresponding values obtained by Fisher's (1928) z transformation. Regression coefficients for the same data are given in Table XII.

A close correlation between carotene and protein has been obtained in previous work and significant coefficients were therefore to be expected; although this was the case with most of the manurial treatments examined, the figures in Table XI show that the degree of correlation varied considerably. Since the significant difference (i.e. twice the standard error) between any two z values is 0.4530, the coefficient of +0.733 obtained for the limed plots did not differ significantly from those obtained with the control or sulphate of potash treatments, but was significantly greater than those obtained with the superphosphate and nitrogenous manures. Although significant, the correlation with sulphate of ammonia

Table XI. *Correlations with carotene*

(z values in brackets)

	Crude protein	Fibre	Ether extract	N-free extract	Ash
No manure	+0.543 (0.6085)	+0.246* (0.2512)	+0.533 (0.5944)	-0.808 (1.1212)	+0.603 (0.6978)
Sulphate of potash	+0.628 (0.7382)	+0.229* (0.2332)	+0.539 (0.6028)	-0.781 (1.0479)	+0.389 (0.4106)
Carbonate of lime	+0.733 (0.9352)	+0.297* (0.3066)	+0.732 (0.9330)	-0.760 (0.9962)	+0.001* (0.0000)
Superphosphate	+0.334 (0.3473)	+0.119* (0.1196)	+0.620 (0.7250)	-0.608 (0.7057)	+0.349 (0.3643)
Nitrate of soda	+0.233* (0.2374)	+0.168* (0.1696)	+0.567 (0.6431)	-0.590 (0.6777)	+0.504 (0.5547)
Sulphate of ammonia	+0.332 (0.3451)	+0.360 (0.3769)	+0.530 (0.5901)	-0.794 (1.0822)	+0.712 (0.8912)

* Not significant.

S.E. of difference of two values of $z = 0.2265$.Table XII. *Regression of ash and organic constituents on carotene*

	Crude protein	Ether extract	N-free extract	Ash
No manure	+0.089	+0.031	-0.203	+0.052
Sulphate of potash	+0.095	+0.030	-0.176	+0.023
Carbonate of lime	+0.147	+0.051	-0.256	+0.0001*
Superphosphate	+0.060	+0.037	-0.139	+0.024
Nitrate of soda	+0.036*	+0.027	-0.111	+0.023
Sulphate of ammonia	+0.053	+0.022	-0.168	+0.039

* Not significant.

was only +0.332, whilst the corresponding figure for nitrate of soda could not be regarded as showing any relationship between the carotene and crude protein in grass under this treatment. Carotene content was thus most closely associated with protein content under manurial treatments which had little or no effect on these two constituents. Under manurial treatments which produced increases in carotene or protein (viz. superphosphate, nitrate of soda and sulphate of ammonia) the correlation between carotene and protein was not so close. These results would seem to indicate that the relationship between carotene and protein is not a direct one, but merely a secondary effect.

The regression of protein on carotene is also seen to vary appreciably with manurial treatment; the highest coefficient was obtained for the limed plots and was significantly greater than the regressions for superphosphate or nitrogenous manures. Since any one fertilizer may affect carotene and protein to different extents, differences in regressions are to be expected.

For grass at various stages of maturity a close negative correlation

has been shown to exist between carotene and fibre (Moon, 1939*b*); with the samples obtained in this investigation, which were cut at regular intervals and thus varied little in respect of maturity, no such relationship was found. Carotene-fibre correlations were calculated for all treatments but were not significant except in the case of sulphate of ammonia, which gave a value of $r = +0.360$. The similarity in the seasonal variations of carotene and fibre is shown by Tables VII and X, and it will be noted that with sulphate of ammonia both carotene and fibre increased consistently from April to August, and decreased in September; the October samples, however, were relatively poor in fibre although very rich in carotene.

Correlation coefficients obtained for carotene and ether extract were similar to the figure of $+0.57$ obtained previously with grass samples of varying age, and there were no significant differences between the various manurial treatments; similarly the regression coefficients did not show any significant variations.

As in the case of ether extract, significant correlations were obtained with nitrogen-free extract and there were no treatment differences. In contrast with the positive correlation between carotene and nitrogen-free extract obtained in a previous investigation (Moon, 1939*b*), a negative relationship is shown in Table XI. Since nitrogen-free extract is a "difference" figure, and since nitrogen-free extract plus fibre constitutes by far the greater part of the dry matter of grass, it follows that any large variations in fibre content will lead to similar but inverse variations in the percentage of nitrogen-free extract; consequently the correlations of carotene with these two fractions would be expected to bear opposite signs, as was the case in this experiment (cf. Table XI) and also in the previous investigation referred to above.

Carotene content has been significantly correlated with ash under all treatments except carbonate of lime. The general tendency for ash to increase with advancing season has already been noted, and since a similar increase occurs in carotene content, the resulting correlation appears to be primarily the effect of the similar seasonal variations in the two constituents. A very heavy dressing of carbonate of lime was applied in March 1939, and resulted in a considerable contamination of the April and May samples; as a result, these had significantly increased ash contents, which probably accounts very largely for the insignificance of the carotene-ash correlation obtained under this treatment. The regression of ash on carotene for the unmanured grass, differed significantly from the regressions obtained with sulphate of potash, nitrate of soda and superphosphate.

The physiological importance of carotene in the plant is not yet understood, but according to present views this pigment does not take a direct part in carbon assimilation. Whilst it has been suggested by various authors that the yellow chloroplast pigments may act as light filters or oxygen carriers, there is little evidence in support of these theories. In view of the provitamin A value of carotene the physiological role of this pigment in the plant and the factors influencing the quantities present, are of some importance; Virtanen *et. al.* (1933) have suggested a relationship between carotene content and growth, but this hypothesis does not readily account for the high carotene content of autumn grass. The correlations calculated in this and other investigations have been obtained in order to provide information on the relationship between carotene and other plant constituents. Such information is still far from complete, but has nevertheless proved quite useful. Thus, the markedly different correlations obtained for fibre and nitrogen-free extract in this investigation and in the previous work with samples of varying age (Moon, 1939*b*), has indicated that such correlations can be largely attributed to well-known variations with season or maturity, and are not likely to have resulted from any close physiological relationship. On the other hand, the similar correlations obtained between carotene and ether extract and between carotene and crude protein in two very different investigations, suggests that in these cases there may be some physiological significance. Further information on these points should be forthcoming when data are obtained under environmental conditions differing from those already studied.

SUMMARY

Sulphate of ammonia and nitrate of soda, applied at monthly intervals, produced increases in the carotene content of poor pasture grass amounting to 28%. Sulphate of potash, also applied monthly, produced an increase of 6.2%. A single dressing of carbonate of lime, which was sufficient to satisfy the lime requirement of the soil, produced no effect on carotene content, whilst monthly dressings of superphosphate also had no influence except in the month of June, when an increase of 14.5% was produced. All five manurial treatments significantly increased the yields of dry matter and carotene.

Carotene contents were very low during the drought experienced in April and May 1938, increased significantly in June, and showed very marked and highly significant increases in the autumn months.

Ash content was increased by the three non-nitrogenous manures,

and protein content by nitrate of soda, sulphate of ammonia and superphosphate. Ether extract was increased by superphosphate and sulphate of ammonia, whilst nitrogen-free extract was decreased under all manurial treatments except carbonate of lime. None of the five artificial fertilizers had any effect on the mean fibre content of the grass, although various significant differences were observed on certain sampling occasions. Normal seasonal variations occurred in the percentages of ash and organic constituents.

Correlations of carotene with crude protein, fibre, nitrogen-free extract and ash have been computed for each manurial treatment and several significant differences have been observed. The physiological significance of these correlations has been briefly discussed.

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MEAT QUALITIES IN THE SHEEP WITH SPECIAL REFERENCE TO SCOTTISH BREEDS AND CROSSES. I

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(With Plates V-XII and Ten Text-figures)

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GENERAL INTRODUCTION

THE breeder and feeder of sheep for meat production is ever faced with the problem of having to modify and improve his animals to be able to cope with changes in demand and to produce the article which will give him the best return. The prime-quality article is usually more expensive to produce than the inferior grades. Unless the consumer is ready to pay that difference the farmer often adopts the policy of producing quantity rather than quality, and by selling more at a lower price aims at obtaining an equivalent return. Improvement of meat qualities in livestock is therefore likely to occur more readily where farmers are producing for a market where the standard of living is high.

In primitive times (Hall, 1936),¹ sheep were kept more for production of wool and milk than meat. In the Middle Ages wool used to be the most important product of English agriculture. With higher standards of living, following the industrial revolution in Great Britain, there has been an increased demand for mutton and lamb. This demand is increasing to-day, while its qualitative nature is also undergoing progressive changes. For example, the present major demand is for small joints of young lamb instead of the large joints of fat, fully matured wethers of some 25-50 years ago. Hirzel (1936) shows the nature of the trend in these changes from 1921 to 1932. During that period Southdowns at 21 months old exhibited in the carcass classes at Smithfield Show had an average carcass weight of 71·8 lb. as compared with 90·8 lb. from 1893 to 1913 and 122·6 lb. from 1840 to 1842 (Hammond, 1921). Hammond & Murray (1934) have shown that weight of the carcass affects price per lb. of mutton, and that a lower price per lb. is obtainable in a heavy carcass than a light one. This price difference is also affected by breed. Prices tend to fall more rapidly with weight increase in early maturing breeds which tend to become excessively fat at high weights (Hirzel, 1936) (see also Part III, § III). Hammond (1937*b*) has illustrated how quality and weight affected the wholesale price of frozen Argentine mutton and lamb in the London Meat Market in the winter of 1937. There is a great difference due to quality, but weight of carcass is, however, of still greater importance. Quality requirements vary greatly in different countries and even in the same country in different districts. In the great cities, London, Birmingham and Manchester, for example, the demand is for lambs of light weights (24-36 lb.) with little fat, while in the smaller towns and in Scotland heavier lamb and mutton are still required. This is illustrated by the fact that the main markets for the large quantities of imported light-weight lambs from countries that specialize in their production are the cities, while, even within Great Britain, London buyers deprive local butchers of all but lambs of the larger breeds. The changes in demand—and these are mainly in weight and fat—can be attributed to three main causes. The small joints are in greater demand due to the smaller families of to-day. Further, there is the natural preference for a small joint two or three times a week rather than one large weekly joint. The demand for less fat meat to-day is the result of the smaller energy requirement of people engaged in mechanized industries and living relatively less active city life. Formerly, when more manual labour had to be employed and the greater proportion of the people lived a rural life,

¹ The list of References will be found at the end of the Second Part.

fat meat could be more adequately dealt with. The quality requirements of the British market are the concern not only of the British farmer, but also of sheep farmers of almost all meat-producing countries, since by far the greatest proportion of the world's mutton and lamb exports are consumed in Great Britain. During the years 1927-30, 93 % of the total world exports of mutton and lamb were imported to Great Britain (Royal Institute of International Affairs, 1932).

In Great Britain, ever since the days of Bakewell, and later in other countries, farmers have been improving their livestock for meat production. Much success has been attained, and some modern breeds like the Southdown sheep and the Aberdeen Angus cattle conform closely to the butcher's ideal. It has, however, remained more an art with individual breeders of pedigree stock to select their animals of highest merit for future breeding rather than a science. Literature on this subject provides abundant evidence of this condition. One often meets with numerous divergent statements and definite opinions about economic qualities in livestock, without any proof being given to support them. The science of genetics has so far largely failed in directly solving the inheritance of important economic qualities in livestock. The animal nutritionalist has done much work on the digestibility of foodstuffs and on the live-weight growth of animals. Until recently little work has been done on the ultimate product of the animal. The work of Lawes & Gilbert (1858) is a notable exception. Later, Waters (1909) in his study of growth and Trowbridge *et al.* (1916-24) in their study of the effect of different planes of nutrition on the development and carcass quality in cattle, have approached the problem from the production side. Hammond (1932), in his intensive study of growth and development of mutton qualities in the sheep, deals with the problem of meat production in a different way from previous workers. He studied the ultimate product meat, and worked backwards to elucidate the conditions or factors which affected its formation. He studied the proportional development of the different parts of the body in sheep with changes in age, weight, breed, and type. In this way he mapped the general trends of growth of the different parts and tissues of the body and demonstrated the fundamental basis for the difference between early-maturing and late-maturing breeds.

It is important but often difficult for a farmer to select a breed which will best suit his purpose. Which breed will give maximum profits under the existing conditions is largely dependent on the market available and the natural conditions of the farm. At present in Great Britain there are some forty distinct breeds of sheep. That some of these differ widely

in respect of such physiological characteristics as hardiness and ability to thrive on a particular type of soil is a well-known fact. But there remains a considerable difference of opinion and lack of definite knowledge of their order of merit in respect of such qualities as early and late maturity, their meat quality and suitability for marketing at certain weights and ages. Until lately little research work has been carried out on these points. One cannot fully rely on comparative literature on this subject, because it is largely based on eye observations of breeders, who often are very familiar with and sometimes prejudiced in favour of a particular breed, without exact knowledge of, or impartiality towards the merits of another. It is a matter of considerable importance to accumulate concrete facts about the breed differences. If these are of economic importance, it can aid the farmer in selecting the most desirable breed.

The main objects of the present investigation are first, to develop a system of measuring carcass quality based on scientific principles, and secondly, to make a comparative study of meat qualities of various breeds and crosses of sheep.

METHODS AND MATERIAL

(a) *Plan of the investigation*

A study of the nature of this investigation is complicated from the outset by the fact that variation in natural conditions, feeding and management occurring between flocks may mask or distort breed differences. Ideally, each breed should be kept under controlled conditions, but such a course is obviously impossible in commercial practice. Nor is it entirely desirable, since in practice environmental conditions vary to an extent beyond the control of man. It is necessary therefore to deal with large samples of sheep selected at random, or with smaller samples drawn from flocks kept under approximately similar conditions. In the present investigation it was impossible to ascertain the precise environmental conditions for the breeds studied. An intermediate course of study was therefore followed. As large numbers of individuals of each breed selected at random as could be dealt with in the time at our disposal were studied. To minimize the effect of variation in environment and husbandry, the following precautions were taken. First, only animals from certain limited areas were studied. Secondly, the breeds were compared at constant carcass weight and approximately the same age. It is reasonable to assume that young growing sheep of different breeds, attaining the same weight at the same age, have done so on

comparable levels of nutrition. A young, growing individual on a high level of nutrition is likely to show this in greater weight for age than another which has been kept on a lower level of nutrition. The absolute breed differences in respect of mutton quality will be demonstrated much more clearly by using the above method of comparison, than by comparing the breeds at the same age regardless of weight. In the latter case one does not know how much of the observed differences are due to weight as distinct from breed. A much heavier carcass, though of the same age as another, is bound to yield certain measurements larger than the lighter one. Bearing in mind that weight of the carcass is even of greater importance in determining its price per lb. than quality (Hammond, 1937*b*), it is of the greatest importance to acquire knowledge at which weight carcasses of the various breeds reach their optimum proportional development, from a carcass quality point of view. The age of the animal within wide limits does not affect the price per lb. of the carcass nearly so much as weight. In the meat trade carcasses of sheep from 3 to 4 up to 8 to 9 months old (for small mountain breeds) are sold in one age class, as lambs, while the same are grouped in several weight classes, and each of the latter is divided into quality grades (Hammond, 1937*b*).

The different breeds were studied as lambs and hoggets. Only wethers (castrated males) have been used for breed comparison, to avoid the possible effect of sex. Carcass weights and measurements of large numbers of individuals from each breed have been recorded. These were grouped in weight classes of 8 lb. (stone of meat) range dressed carcass weight, the ages being kept separate. The weight range of a stone was thought suitable, since it is much used in the commercial classification in the meat trade and at the same time is sufficiently small not to cause too great variations in measurements due to weight differences within a weight class. The breed differences in respect of various factors affecting their meat quality based on these data have been analysed statistically. The changes in the various measurements with increase in weight and age within any one breed have also been studied. Both angles are dealt with in Part II. To acquire more exact knowledge about the breed differences in respect of proportional development of the different parts of the body and the composition by weight of the same than is obtainable from linear measurements of the carcass, it was decided to dissect anatomically a few carcasses for detailed study of these factors. For this purpose a carcass of one lamb and one hogget of each breed under investigation was selected. These were at a constant weight in each case.

To ensure that these individuals were typical of their breed they were chosen so that their carcass measurements approached as nearly as possible the average measurements of the particular weight class of the breeds concerned. It must be admitted that the use of a single animal as a representative of a breed is not a very reliable basis for breed comparisons, due to the possibility of considerable individuality within a breed. However, when this animal closely approaches the mean of a number of individuals of the same breed, age and weight in respect of several major characteristics, it is of much greater value than an animal selected by chance.

Since a complete dissection of carcasses is both very laborious and expensive and funds were not available for the purchase and dissection of large numbers of carcasses, the method here adopted was the only one possible. The results of this part of the work are described in Part III. The data from the dissected animals have also been used to study the value of various carcass measurements as indices to quality and composition of hogget and lamb carcasses. Information of this nature is of considerable importance. If measurements of the carcass are not correlated with quality and composition, the present work, as well as results from previous workers, who have based their studies of breed differences (Hirzel, 1936) and growth (Meek, 1901; and several others) on body or carcass measurements, is relatively useless from a practical point of view. Any future work on the same lines would likewise be futile. On the other hand, if some of the measurements were found to be a reliable indication of carcass quality and composition, it would greatly enhance the value of past and present work on these lines, as well as making it possible to construct a scale of points for judging mutton and lamb based on scientific principles. The possibility of using "sample joints" for estimating the composition of the total carcass has also been investigated, as a means of easing the task of the research worker interested in the effect of breed and treatment on the growth and composition of the animal body. This is described in Part I.

(b) *Material*

The major part of the work was carried out in Edinburgh. The following breeds and crosses were studied: The Border Leicester \times Cheviot (Half-bred), Border Leicester \times Blackfaced (Greyface), Oxford \times Border Leicester-Cheviot, Suffolk \times Border Leicester-Cheviot, Southdown \times Border Leicester-Cheviot, Cheviot and Scotch Blackfaced. In addition data on the Suffolk sheep were obtained at Cambridge. The native

Iceland breed and its cross with the Border Leicester were studied in Akureyri, Iceland.

All sheep used in this investigation were commercial animals. They had been bred and fed on various farms in the districts mentioned below. The Scottish breeds were derived from the east and south-east of Scotland, mainly the following districts: the Lothians, Peebleshire, the Borders, Berwickshire and Fifeshire. Some of the hoggets may have been bred in the north-east of Scotland, particularly the Border Leicester \times Cheviot cross, which is bred on a large scale in Caithness, Sutherland and elsewhere in the north. These are sold as store lambs for hoggeting in the arable districts farther south. A system of selection was adopted to ensure that the sheep studied would be as truly representative of their breeds as one could expect to get in a field investigation. A few of the largest butchers in Edinburgh generously permitted the work to be carried out on the sheep they bought from farmers in the local Fat Stock Market for retail trade in the town. Only animals exhibiting definite breed characteristics were used. Any "mongrels" or individuals of doubtful cross-breeding were excluded. Likewise animals in abnormal conditions due to disease, accidents or other causes were avoided. The animals were bought in lots of small numbers, varying from one to sometimes over twenty, as is customary in British Fat Stock Markets. Therefore the sheep bought by a butcher in one day often came from several farms. From these, numbers of individuals of the right breed and age were selected at random for study each week. The approximate age of the individual animals was estimated from the time of lambing for each breed in this district, and the date of killing. Lambs were studied at approximately 4-5 months and hoggets from about 10 to 13 months of age. Though there must be considerable difference in age of the individuals studied, this will not affect the breed differences seriously. The effect of one breed having an earlier lambing season than another is largely nullified by the fact that animals of the early lambing breeds come to the butcher correspondingly earlier than those from the breeds which lamb later (see Appendix VIII).

The Suffolk hoggets referred to in this investigation were all bought by a Cambridge butcher in the local Fat Stock Market. They were studied during late December and January. They are of comparable age with the Scottish hoggets, because lambing in Cambridgeshire begins correspondingly earlier than in Scotland. The Iceland and Border Leicester \times Iceland lambs included in this work were born in late May and beginning of June and killed in the end of September. They are therefore slightly younger than the Scottish lambs.

(c) *Methods of investigation and technique employed*

Carcass weight. The carcasses were weighed after having been allowed to cool for 10–20 hr. on the rails in the abattoir. When the head was left on the carcass an estimated allowance for it was deducted from the gross carcass weight. This was done by weighing a number of heads of sheep of different breeds and weights. Heads of lambs averaged slightly under 4 lb. They ranged from 3 lb. for light lambs of small-boned breeds up to 5 lb. for heavy lambs of large-framed breeds. The average weight of a head of a yearling sheep was 5 lb. It varied from *ca.* 4 lb. to over 6 lb., depending on breed and weight. Occasionally carcasses had to be weighed warm immediately after slaughter. The normal loss of weight due to evaporation of moisture during cooling was estimated by weighing a number of carcasses warm and again after the normal periods of cooling. The loss varied from $\frac{3}{4}$ to 2 lb. A lean carcass lost more than a fat one. The average loss was just over 1 lb. This agrees with Hammond's results (1932). In summer lambs lost as much weight during cooling as hoggets in winter. Since the lamb carcasses were lighter than those of the hoggets the percentage loss was higher in the lambs. This can be attributed to warmer atmosphere in summer and the lambs being leaner than the hoggets. Carcass weight referred to hereafter, except where otherwise stated, indicates the weight of cold dressed carcass, without head and feet.

Carcass measurements. Large numbers of different measurements on the carcass were recorded. Linear measurements were taken in the main with a linen tape scaled in millimetres. Short distances were measured by steel dividers and scaled off on a wooden millimetre scale. Such measurements as depth of thorax, width and depth of gigots were taken by special sliding callipers. The number of ribs on both sides of every carcass was recorded. Text-fig. 1 illustrates the position of the various measurements on the carcass.

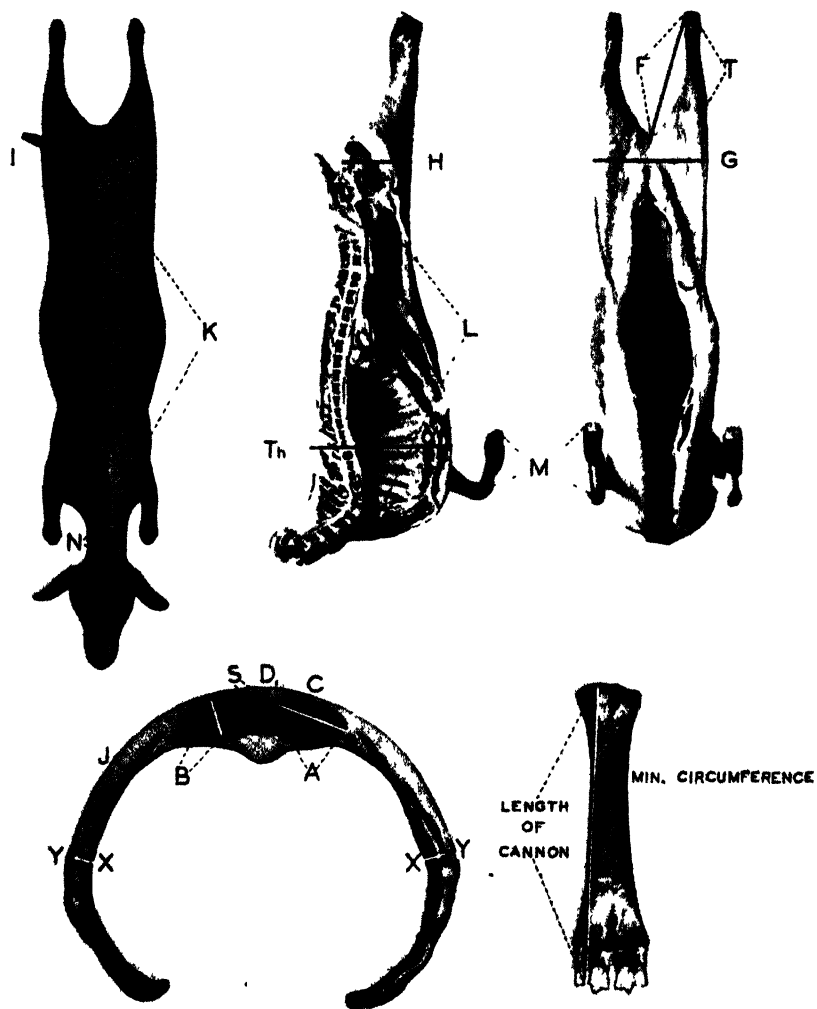
(i) The following external measurements were taken on the carcass hanging in the abattoir, suspended from a gamble of constant width:

F = leg length.

G = width of gigots.

H = depth of gigots.

I = fullness of thighs. From a point just below the patella on one side, the tape was passed under the tail to a corresponding point on the other side.



Text-fig. 1. Carcass measurements.

K = length of body from the tail head to the base of neck.

L = length of body from the symphysis pubis to the anterior edge of the middle of the first rib.

M = length of the fore cannon (metacarpal).

N = length of neck.

R = length of radius-ulna from the olecranon process to the styloid process.

T = length of tibia + tarsus from the tubercle on the proximal end of the tibia to the anterior edge of the distal end of the tarsal.

Th = depth of thorax. The maximum depth of chest behind the shoulders.
Measurements N and Th were only taken on the lambs.

At the time of killing every carcass was labelled with a specific number to enable one to identify it later in the butcher's shop. There the carcasses were divided into two portions by a cut vertically through the flank to the anterior edge of the last rib on each side. Then the curve of the ribs was followed to the vertebral column where the latter was severed at the junction of the last and second to last thoracic vertebrae. The last thoracic vertebra was therefore left on the hindquarters.

(ii) The following measurements were recorded from the anterior surface of this section. Both sides were measured and the average used:

A = "length" of "eye muscle"—the maximum distance across the cross-section surface of the longissimus dorsi from the end next the spinal process outwards along the rib.

B = depth of "eye muscle"—the greatest distance at right angles to A on the same surface.

C = thickness of back-fat over the deepest part of the "eye muscle".

D = thickness of fat over the spinous process.

J = thickest layer of fat over rib at the point illustrated.

S = length of spinous process of second but last thoracic vertebra.

X = thickness of muscle layer (mixed with fat) on lower half of rib at point illustrated.

Y = thickness of subcutaneous fat layer over X .

Colour of eye muscle. The colour was measured by eye on a special colour chart.

The left fore-cannon bone (metacarpal) of each sheep was carefully cleaned off its tendons by a scalpel and weighed. Its length and minimum

circumference were measured as illustrated in Text-fig. 1. The former was taken by sliding callipers, but the latter by a narrow linen tape.

Dissection technique. The live weight prior to killing and the weight of warm carcass with head were recorded. All the external carcass measurements enumerated above were taken.

The carcasses had to be taken from Edinburgh to Cambridge for dissection. The animals were killed in the forenoon and the carcasses allowed to cool for 3–8 hr. in a cold chamber. In the afternoon they were carefully packed in a large wooden box in order that they might retain their normal shape. They were taken on the night train from Edinburgh to Cambridge, arriving there in the early morning. The cold carcass weight could not always be obtained in Edinburgh. Their cold weight on arrival at Cambridge was recorded. A photograph of the dorsal view of each carcass, hanging from a beam, suspended from a gamble of constant width, was taken. Subsequently the carcass was cut through in front of the last rib as described above. The anterior surface of this cross-section was then photographed and the various measurements referred to above were recorded. Individual measurements of each carcass dissected are recorded in Appendix II. All measurements were taken in duplicate.

Jointing the carcass. It was a matter of great importance to adopt a standard method of jointing the carcass. Any lack of uniformity in this direction could result in errors in the study of proportional development of the different parts of the body. The method used by Hammond (1932) was followed with slight modifications. He jointed the carcass anatomically rather than according to "butchers' joints". Though the latter method may be desirable from a purely practical point of view, it involves cutting through several bones. This cannot be done accurately, and the bones are damaged for any special study. Further, butchers in different countries and even in different districts do not follow the same rule in jointing the carcass. In dividing the carcass anatomically the bones provide the major fixed cutting points. To minimize errors which may occur in cutting through the soft tissues the work was performed by the same skilled persons whenever possible. After the kidneys and loose internal fat surrounding them was removed prior to cutting through the carcass at the last rib the carcass was divided into the following joints:

The *Head* was severed at its articulation with the atlas.

The *Shoulders* were cut off by first severing the muscles attaching these to the sternum. Then by traction on the arm the shoulder was separated from the thorax. A knife was then drawn round the scapula,

severing the latissimus dorsi muscles, and almost reaching the mid-line of the thoracic vertebrae. From there the knife was carried forward round the scapula to the base of the neck, cutting through the trapezius and brachiocephali muscles.

The *Neck* was separated from the thorax at the junction of the cervical and thoracic vertebrae. The last thoracic vertebra, which had been left attached to the loin when the carcass was divided, was removed by a transverse cut behind the last rib, and added to the thorax.

The *Loin* was divided from the gigots by a transverse cut on each side, at the level of the anterior extremity of the ilium wing (hip bones). The inside curve of the latter was then followed and the vertebral column severed at the junction of the last lumbar vertebrae with the sacrum.

The *Legs*. A transverse cut was made directly through the muscles at the level of the anterior edge of the symphysis pubis. The two legs were then separated by a cut along the posterior median line to the symphysis ischium, laying bare the surface of the gracilis muscles on each side. The femur-acetabulum joint was then severed. Working from the symphysis ischium, the gracilis and adductor muscles were separated from the ventral surface of the ischium. The ischial arch and the postero-lateral angle were then followed to the acetabular branch of the ischium, working as close to the bone as possible and severing the biceps femoris and semi-tendinosus muscles at their attachments. A circular cut was then made from the acetabulum through the musculature of the thigh to meet that previously made from the flank at the level of the symphysis pubis.

The remaining joint constituted the *Pelvis*.

Hammond (1932) did not deal with the pelvis as a separate joint, but divided the gigots along the median line into the two "legs". Therefore, one has to add one-half of the weight of the pelvis on to each leg to make these comparable with the "legs" in Hammond's work.

Immediately after each joint was separated from the body it was weighed and wrapped in cold moist towelling. Joints which could not be worked on at once by the available staff were placed in a cold store to await dissection.

(d) *Dissection of joints*

Each joint was dissected into its main components, bone, muscle, subcutaneous fat, intermuscular fat, glands, and tendon. The various organs of the head were separated. In the feet the bones were dissected out and the remainder, skin, hoof and tendon, was weighed in bulk.

Weight of each ingredient was recorded in grams. In the limb joints the muscles and intermuscular fat round the radius-ulna in the forelimb and round the tibia-fibula of the hindlimb were weighed separately from the same ingredients of the upper part of the limbs. Bones were weighed either individually or in groups, depending on the bone concerned. A sample of muscle taken from the longissimus dorsi over the last rib was placed in 10 % formalin solution for histological work and estimation of the amount of marbling fat. Details of weight of joints and their constituents can be obtained from Appendices III, IV and V.

The process of dissection of a typical joint was as follows:

The joint was placed on a dissecting board covered with a damp cloth. To minimize moisture losses during dissection the joint itself and its various parts when separated were kept under cold moist towels throughout the process. Any direct handling of the meat was avoided by use of forceps. The subcutaneous fat was first completely removed by a scalpel and forceps. Subsequently the muscle and intermuscular fat were carefully separated from the bones in a bulk. The bones were then wrapped in moist cloth, while the muscles were carefully separated and any fat between them removed by scissors and forceps. Any glands were separated from the fat. The bones were then cleaned. Any muscle adhering to the bones was removed and added to the muscle of the joint. The tendons attached to the bones were cut away. All cartilage was left on the bones. Individual bones—and indeed all parts—were weighed as they were cleaned to minimize evaporation losses. Further precautions in this direction were taken by aiming at finishing each joint in as short a time as possible by dividing its ingredients between sets of workers. By the help of the trained staff of the School of Agriculture and several others interested, to all of whom our thanks are due, the dissection of each carcass was completed in a day. A staff of six trained people, working from 12 to 14 hr. a day, were required to complete a carcass.

The results were extremely satisfactory. The loss during dissection was very small (see Appendices I and III). Hammond (1932) in the sheep, McMeekan (1938) in the pig, lost more weight during dissection than was the case here, though most of the work was done by the same people and the same technique used. This can be explained by the fact that the carcasses had lost more weight during transport from Edinburgh than normally for the same period. If that had not been the case most of the moisture lost during transport would have been lost during dissection, making the results agree.

PART I. CARCASS MEASUREMENTS AND "SAMPLE JOINTS" AS INDICES OF QUALITY AND COMPOSITION

INTRODUCTION

The quality of mutton and lamb carcasses at any weight depends chiefly on their age, conformation and composition in terms of bone, muscle, fat, and offals.

It is well known that age affects texture and flavour of the meat as well as composition (Hammond, 1932).

Old animals have coarser, darker and stronger flavoured meat than young ones. Increase in age up to a certain limit has beneficial effects upon composition of the carcass. Very young animals are usually too lean and have a high proportion of bone to edible meat, while the reverse is true of more mature animals. The optimum age of slaughter depends greatly upon breed and nutrition. Well-fed animals of early maturing breeds are ready for the butcher at a young age, while late-maturing animals or poorly fed ones may lack "finish" until at much greater age.

Conformation of the animal is of great importance from the butcher's point of view. Some parts of the body (loin, legs) are more valuable to him than others (neck), so that the value of the animal depends on the proportions of these in the carcass.

The bones should be thickly covered with meat and the joints compact. A short thick leg is more valuable than a long narrow one of the same weight and composition. The latter is inclined to dry out in the process of storage and cooking because of its large surface and relatively thin fat cover, while the flesh of the former remains juicy and tender after cooking. Moreover, as will be shown later, a long leg has usually a higher proportion of bone to muscle and fat than a short leg of the same weight.

The food value of meat depends necessarily on its chemical composition. The price per lb., however, is affected more by the nature of the joint, how it can be cooked, the proportion of muscle to bone, and the state of fatness, than by the chemical composition.

The ideal joint is one with a high proportion of muscle to bone and a sufficient cover of subcutaneous fat to prevent it from undue drying on storage and cooking. Excess fat is objectionable and wasteful. It is expensive to produce but is only of value as suet. An excessively fat carcass is thus worth less per lb. than one in an optimum state of fatness.

For more detailed account of the conception of carcass quality see Hammond (1937*a*).

Body and carcass measurements have been used by numerous workers in the comparison of breeds and the study of growth changes. Hammond (1932), in his study of "Growth and development of mutton qualities in the sheep", did not use carcass measurements. He claims that though such measurements have done much to indicate length growth in bones, they do not show conclusively that either bone thickness or muscular growth follows the same way. Later, however, Hammond (Hirzel, 1936) adopted a system of measuring the development of muscle and fat in sheep as seen in cross-section of the carcass at the last rib. Hirzel, analysing data on the sheep exhibited in the carcass classes at the Smithfield Show, has demonstrated the optimum degree of development of muscle and fat in this region from the quality point of view. This he based on the actual measurements of the prizewinners and champions as compared with those which did not receive an award.

Carcass measurements have been used in several countries for grading pig carcasses. It is easier to grade these on a basis of "internal" measurements than is the case with sheep carcasses, because the former are usually split along the back, so exposing the thickness of the back-fat.

Hankins & Ellis (1934) correlated carcass measurements in pigs with composition of the carcass and found a high correlation between back-fat measurement and total fat (by chemical analysis) in the edible parts of the pig.

For sheep no such work has been done. In § I we aim at showing how far carcass measurements can be used as indices of composition and quality of the carcass.

§ II deals with the possibility of estimating composition of mutton and lamb carcasses by the use of "sample joints".

MATERIAL AND METHODS

The material consisted of eleven wether lambs and five wether hoggets of different breeds. The lambs were selected at approximately 4½ months old and 40 lb. dressed carcass. The hoggets were approximately 13 months old with 60 lb. dressed carcass. For breed, origin and exact weight see Appendix I.

The carcasses were measured, jointed and dissected as described above (p. 551). The raw data are given in Appendices II-V.

The lambs, due to their great breed differences, provide particularly

useful material for this work. They are representative of vastly different breeds, from the highly esteemed New Zealand Southdown \times Romney to the inferior Oxford \times Border Leicester-Cheviot, and the native Iceland breed, relatively unimproved for meat production. In consequence, any relationship established between measurements and composition is likely to hold good for lambs of any meat-producing breed, at comparable age and weight. In practice the effect of even considerable differences in age or environment, on animals of any one breed, is unlikely to result in greater differences in conformation or composition of the carcass.

The hoggets are unfortunately so few that correlations between their measurements and composition are liable to large sampling errors. They are representative of more related breeds and therefore show less variation.

The value of the various measurements taken has been examined by correlating these with carcass composition and other factors affecting carcass quality (head, feet and kidney fat were excluded in all the calculations). Similarly in § II the relationship between the composition of sample joints and that of the whole carcass has been worked out.

Fisher's (1936) method for calculating the correlations and regression coefficients has been used.

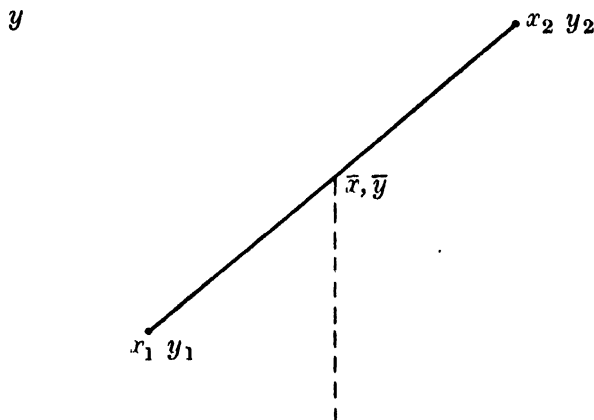
In most cases a rough diagram was plotted to see the trend of the relationship between the variates. Only where this relationship was marked has the correlation coefficient been calculated.

For those cases where very strong relationship existed between the variates the regression coefficients and regression equations were calculated. Lambs and hoggets have been dealt with separately. It is of importance, however, to know something of the relationship between measurements and composition for the weight and age range between lambs and hoggets. Since it cannot be assumed that increase in measurements with weight and age is strictly linear—the nature of biological relationship is against such an assumption—it has been considered unsound to lump the data for lambs and hoggets in an endeavour to cover carcasses of intermediate age and weight.

The difficulty has been overcome by calculating the regressions between the variates at a constant age (lambs and hoggets separately), and where these do not differ significantly, by calculating the correlation and regression coefficients within ages. This gives the best estimate of the slope of the regression between the variates at any age and weight within the limits of the data (40–60 lb.).

To obtain a complete regression to which animals of intermediate

ages and weight may be referred we require the averages of both variates for such intermediate classes. Approximations to these averages may be calculated from the available data as shown in the graph below:



It will be seen from the graph that if \bar{x} be the average value for the independent variable for animals of an intermediate weight class \bar{y} will be

$$\bar{y} = y_1 + \frac{(y_2 - y_1)(\bar{x} - x_1)}{(x_2 - x_1)},$$

where $x_1 y_1$ and $x_2 y_2$ are the mean values of the variates in lambs and hoggets respectively.

§ I. MEASUREMENTS AS INDICES OF CARCASS COMPOSITION AND QUALITY

A. MEASUREMENTS AS INDICES OF THE WEIGHT OF BONE

(1) *External measurements*

External carcass measurements do essentially give an idea of the development of the skeletal framework of the animal. Some are a direct measure of the length of the bone, such as *T*, the length of tibia and tarsus. Others, such as *F*, *L*, *Th* and *N*, give a very useful picture of the conformation of the carcass, but do not measure length or thickness of any individual bones and are affected, particularly the leg length *F*, by the development of muscle and fat.

The weight of a bone depends on its length, thickness and density. In the limb bones, which make up a great part of the weight of bone in the carcass, length growth is likely to contribute more to their weight

than thickness growth. However, breeds differ considerably in bone thickness (see Hammond (1932), Nathusius (1880) and Parts II and III of this paper).

Therefore one cannot expect a perfect correlation between a length measurement of any bones and the weight of the skeleton.

The length of tibia and tarsus T is the only external carcass measurement taken which shows a strong relationship with the weight of the skeleton.

Table 1 shows the correlation between various measurements and the weight of skeleton (skull and bones of feet excluded).

Table 1. *Correlation between measurements and weight of skeleton (head and feet excluded)*

Population	No. of pairs	Measurement Independent variate $-X$	Dependent variate (weight of skeleton) = Y			
			Correlation coeff.	P	Regression coeff. Y, X	Regression equation
Lambs	11	T	0.821	<0.01	15.12	$Y = 15.12X - 792$
	9	Length of left fore-cannon	0.754	<0.02	19.02	$Y = 19.02X + 48.6$
	9	Weight of left fore-cannon	0.9432	<0.01	46.64	$Y = 46.64X + 333$
	9	Weight of four cannons	0.9594	<0.01	10.4	$Y = 10.4X + 518$
	9	$\frac{\text{Weight}}{\text{Length}} \times 100$ of left fore-cannon	0.7466	<0.05	74.83	—
Hoggets	5	T	0.610	>0.05	—	—
	5	Length of left fore-cannon	0.805	>0.05	—	—
	5	Weight of left fore-cannon	0.9809	<0.01	42.09	$Y = 42.09X + 930$
	5	Weight of four cannons	0.973	<0.01	11.0	$Y = 11.1X + 787$
	5	$\frac{\text{Weight}}{\text{Length}} \times 100$ of left fore-cannon	0.9790	<0.01	68.1	$Y = 68.1X + 352$
Within ages, lambs and hoggets	14	Weight of left fore-cannon	0.9600	<0.01	44.164	—
	14	Weight of four cannons	—	—	10.744	—
	14	$\frac{\text{Weight}}{\text{Length}} \times 100$ of left fore-cannon	—	—	69.61	—

Length of tibia and tarsus has a highly significant positive correlation at the 1% level in lambs. In hoggets the correlation is not significant at the 5% level. This may be due to a sampling error in the hoggets which are only five in number. The fact that length growth in bones is an early developing character as compared with thickness growth is most likely another factor contributing to the lower correlation in hoggets. At 4.5 months the tibia is still actively growing in length, while at about a year old it has practically reached its ultimate length, while it is still actively growing in thickness (Hammond, 1932). The approximate weight of bone in a lamb carcass of 40 lb. and 4.5 months of age can be estimated from the regression equations (Table I).

It is of importance that any measurement, which is to be used for

estimating carcass composition, can be accurately taken. The length of tibia and tarsus can be taken with great preciseness to a millimetre. Tables 11 and 12 show the averages of this measurement for different breeds. The standard error per sheep is only 3.4 % of the grand mean.

(2) *The cannon bone*

For practical reasons it is of value to be able to estimate the weight of bone in the saleable parts of the body from measurements or weights of bones in the offals (feet). Hammond (1932) suggests that for estimation purposes the femur as a late developing bone is likely to be suitable. Practical considerations, however, prevent the use of this bone, as it is situated deep in the carcass. Therefore he suggested the use of the cannon bones for this purpose, as they can be obtained without damaging the carcass and can be easily cleaned. Moreover, as four exist in the carcass an average could be taken to ensure greater accuracy. He worked out the ratio: weight of total bones in carcass over weight of one cannon in animals of different breeds at various ages, concluding that variations in this ratio are great when different ages are concerned, but are close enough for practical purposes when the ages are not very different. This is due to the fact that the cannon bones develop early in life as compared with most other bones in the body, and their postnatal growth as a percentage of their weight at birth is less than in other regions (loin, pelvis) (Hammond, 1932).

We have correlated the length, weight and the weight : length ratio of the left fore-cannon (left metacarpal) as well as the weight of all four cannons with the weight of total bone in the carcass, and obtained extremely satisfactory results (Table 1). The length of cannon is not quite so strongly correlated with the total weight of bone as is the length of tibia. This can be expected, as the cannon is slightly earlier developing and absolutely shorter than the tibia. The difference between these correlations is, however, so small that one is justified in using either as suits the case.

The weight of the four cannons is extremely highly correlated with skeletal weight, both in lambs and hoggets. The relationship between the weight of the left fore-cannon and the total weight of bone in the carcass is quite as good as when all the four cannons are used, so that with careful work the use of one only is justifiable. Table 1 shows that regression coefficient for weight of skeleton on weight of left fore-cannon is lower for hoggets than lambs, indicating less slope of the regression line. The opposite is the case for the four cannon bones. This may be due to the

relatively greater thickness development in the fore-cannons with age as compared with the hind-cannons, which remain relatively slender. The weight per 10 cm. $\left(\frac{\text{weight g.}}{\text{length mm.}} \times 100 \right)$ of the left fore-cannon is correlated with weight of bone in the carcass.

For lambs, however, the correlation is only significant at the 5 % level, while in hoggets it is highly significant at the 1 % level. This is a direct result of the fact that thickness growth in bones is a relatively late developing character as compared with the length growth. At 1 year old bone thickness contributed relatively more to the weight of skeleton than at 4-5 months of age, while at the younger age the length of the bones has a greater influence on the weight of the skeleton than at the higher age.

The best single measure we have found for estimating the weight of total bone in the carcass is therefore the weight of one fore-cannon. This gives at both ages a very accurate estimate.

B. MEASUREMENTS AS INDICES OF THE AMOUNT OF MUSCLE

(1) *External measurements*

As stated above, external carcass measurements are essentially more indicative of skeletal size—length of bones—than of muscle or fat development.

Due to this fact we have not been able to find a high correlation between any external carcass measurement and the weight of total muscle in the body. Bone, though growing simultaneously with muscle, attains more of its ultimate development early in life than the latter (Hammond, 1932). A large late-maturing animal, at the same weight and age as a small early-maturing one, though having most external measurements higher than the latter, may have less muscle due to the larger development of the skeleton.

Since the weight of the bones in a carcass can be estimated with a high degree of accuracy, correlation between measurements and the weight of muscle as a percentage of the skeletal weight could be of equal practical value to direct correlations for estimation purposes, and if higher than the latter would provide the basis for more reliable estimates. One of the main factors affecting the muscle : bone ratio is the thickness of muscle cover.

The difference between the leg length and the length of tibia and tarsus ($F - T$) gives a very good idea of the development of the muscu-

lature round the femurs and between the legs. The smaller this difference, the thicker is the muscle cover and the better is the gap between the legs filled with meat.

There is a high negative correlation between $F-T$ in the lambs (Table 2). In the hoggets this correlation is also negative but not significant at the 5% level, possibly due to the small numbers represented. The width of gigots (G) expressed as a percentage of the length of the leg (F) $\frac{(G \times 100)}{F}$, which is a good index of the compactness of the hind-quarters, has a high positive correlation with the weight of muscle expressed as a percentage of the bone weight in lambs. For the hoggets this correlation is not significant (see Table 2).

Table 2. *Correlation between measurements and weight of muscle in carcass expressed as percentage of the weight of skeleton (head and feet excluded)*

Dependent variate (muscle as % of skeletal weight) = Y						
Population	No. of pairs	Measurement Independent variate = X	Correlation coeff.	P	Regression coeff. Y, X	Regression equation
Lambs	11	$F-T$	-0.9331	<0.01	-3.37	$Y = 605 - 3.37 X$
	11	$G/F \times 100$	0.8690	<0.01	—	—
	11	$B/A \times 100$	0.8000	<0.01	—	—
	11	B	0.7136	<0.02	—	—
Hoggets	5	$F-T$	-0.5275	>0.05	—	—
	5	$G/F \times 100$	0.4457	>0.05	—	—
	5	$B/A \times 100$	0.6195	>0.05	—	—
	5	B	0.6685	>0.05	—	—

(2) *Internal measurements*

The development of the animal for meat purposes can be estimated most effectively by cutting the carcass at the last rib and observing the development found there (Hammond, 1937c). Hammond verifies this by the fact that the main growth gradients in the body of the sheep, a primary wave of growth spreading outwards from the cranium towards the lumbar region and to the facial parts and secondary growth waves spreading upwards from the distal ends of the limbs and from the caudal area, all meet in the region of the lumbar and thoracic vertebrae (Hammond, 1932). Another important reason is that the loin constitutes the most valuable part of the carcass.

We have calculated the correlation between various linear measurements on the cross-section surface of the muscles at the last rib with the weight of total muscle in the carcass (Table 3).

Length of "eye muscle" (longissimus dorsi) A is correlated with the

weight of muscle in the carcass, though, due to the small numbers, it is only significant in lambs at the 5% level and is not significant in hoggets. Length of "eye muscle" is an early developing character (Hirzel, 1936). Therefore it should contribute more to the weight of muscle early in life than later, when muscle grows more actively in thickness. This explains why *A* is more highly correlated with weight of muscle in the lambs than the hoggets, while the reverse is the case with *B* (depth of "eye muscle"). Measurement *B* is correlated with the weight of muscle in the carcass but not significantly so for the small numbers concerned. This is probably due to the different proportional development of the various breeds. With breed improvement the most valuable parts of the body (loin, pelvis, legs) have been increased in weight relative to the less valuable cuts (neck, chest). In the improved breeds like Southdown \times Border Leicester-Cheviot *B* is large, while in the inferior Oxford \times Border Leicester-Cheviot or Iceland this measurement is relatively small (Parts II and III). The latter breeds, however, have heavier necks and shanks than the improved ones, so the absolute difference in weight of muscle in the carcass is not so great as the difference in the depth of the "eye muscle".

Table 3. *Correlation between measurements and weight of muscle in carcass (head and feet excluded)*

Population	No. of pairs	Dependent variate (weight of muscle g.) = <i>Y</i>				
		Measurement Independent variate = <i>X</i>	Correlation coeff.	<i>P</i>	Regression coeff. <i>F, X</i>	Regression equation
Lambs	11	<i>A</i>	0.6744	<0.05	—	—
	11	<i>B</i>	0.4681	>0.05	—	—
	11	<i>A + B</i>	0.7721	<0.01	145.7	—
	11	<i>A + B + X</i>	0.6137	<0.05	—	—
	11	<i>A + 2B</i>	0.7049	<0.02	90.26	$Y = 90.26.X - 764$
	11	<i>2A + B</i>	0.7683	<0.01	88.09	$Y = 88.09.X - 3146$
	11	<i>B/A \times 100</i>	0.0675	<0.01	—	—
	11	<i>L/10 + A + B</i>	0.8002	<0.01	119.58	$Y = 119.58.X - 7714$
Hoggets	5	<i>A</i>	0.4971	>0.05	—	—
	5	<i>B</i>	0.5986	>0.05	—	—
	5	<i>A + B</i>	0.8056	>0.05	—	—
	5	<i>A + B + X</i>	0.8960	<0.05	170.6	$Y = 170.6.X - 3940$
	5	<i>A + 2B</i>	0.7575	>0.05	—	—
	5	<i>2A + B</i>	0.7316	>0.05	—	—
	5	<i>L/10 + A + B</i>	0.8997	<0.05	164.56	$Y = 164.56.X - 11768$
Within ages	16	<i>L/10 + A + B</i>	0.8346	<0.01	134.865	—

Because the length of "eye muscle" *A* is relatively large in the unimproved breeds, we have calculated the correlation between various combinations of these measurements and the weight of muscle. The results are given in Table 3. In every case except one the correlations between these combinations of the muscle measurements and weight of

muscle in carcass are higher than when A or B alone were used. For lambs, $A + B$ and $2A + B$ give the highest correlation, which is highly significant at the 1% point. In hoggets, due to the small number of these, none of the correlations for the "eye muscle" measurements alone are significant. B , however, has more effect on improving the correlation in the hoggets than in the lambs, which can be expected because of its later development. When X (the thickness of the muscular layer on lower half of the rib) is added to $A + B$, the correlation between the sum of these measurements and weight of muscle in the carcass is significant both in lambs and hoggets, but higher in the latter case. The shape index of the "eye muscle" $\left(\frac{B \times 100}{A}\right)$, which is an important quality measurement (see later), has no relationship whatsoever with the weight of muscle in the body.

It must be realized that the body length must contribute to the weight of the muscle in the carcass as well as the thickness of the muscles. Therefore we have added the body length in cm. to $A + B$ in mm. and correlated the sum of these measurements with the weight of the muscles in the carcass. This correlation is significant both in the case of lambs and hoggets (Table 3).

Since depth of "eye muscle" B is a definite measure of thickness of muscle at a late developing point in the body, it could be expected to be correlated with muscle expressed as a percentage of the bone weight. Therefore the correlation between B alone and B expressed as a percentage of the length of "eye muscle" A (shape index) with weight of muscle as a percentage of bone weight in the carcass has been calculated (Table 2).

Both correlations are significant in the lambs.

C. MEASUREMENTS AS INDICES OF THE WEIGHT OF FAT

(1) *External measurements*

It is often extremely difficult to judge by eye with any degree of accuracy the state of fatness of a carcass. No external carcass measurements are directly correlated with the weight of fat in the body. There is, however, a high significant negative correlation between the leg length F and the weight of fat expressed as a percentage of the weight of the bones in the carcass, both in lambs and hoggets (Table 4).

(2) *Internal measurements*

The various linear measurements of the fat development on the cross-section surface of the carcass at the last ribs have been found to be significantly correlated with the weight of fat in the body (Table 4). D , the depth of fat over the spinous process, was the only fat measurement taken which is not highly correlated with weight of fat. The thickness of fat over the "eye muscle" C , which is a late-maturing character, is very highly correlated with weight of body-fat in hoggets but to a lesser extent in lambs. This again confirms the fact that a measure of a late-developing character is not as good a guide to composition of the body early in life as later.

The sum of the three best fat measurements ($C + J + Y$) is highly correlated with weight of body fat at both ages. Unfortunately these fat measurements cannot be taken with the same degree of accuracy as can measurements of muscle and bone. The absolute value of C and Y is usually only a few millimetres; the error involved in recording only to the nearest millimetre is therefore considerable. The error is diminished by taking an average on both sides.

By the use of the regression equations of Table 4, one can estimate the approximate amount of fat in carcasses of lambs and hoggets at the ages and weights concerned.

The error involved is mainly due to breed differences. The weight of fat in the carcass of an early-maturing animal which has already attained a high degree of development in the loin region will be over-estimated by the use of these measurements, while it will be under-estimated in a late-maturing animal. The latter may have much fat in the neck and on the sternum, but relatively less in the loin region, while the opposite is true of the former. We believe that the correlation between these measurements and the weight of fat in the body is much higher within a breed or within related breeds. The weight of fat in the carcass is essentially affected by its size as well as the thickness of the fat cover at any point. Therefore we have calculated the relationship between total fat and such combinations of the measurements as will give an approximation of the volume of subcutaneous fat cover in the carcass (Table 4). The sum of the fat measures at the last rib times the body length L shows the highest relationship. In the hoggets this correlation is extremely high and reasonably satisfactory for estimation purposes in the lambs.

In all cases but one the correlation between the various measure-

ments and fat are higher in hoggets than lambs. This is due to the fact that fat measurements at the last rib are primarily measures of the thickness of subcutaneous fat, which increases at a greater rate later in life than does intermuscular fat (McMeekan, 1938).

Table 4. *Correlation between measurements and weight of fat in carcass (head, feet and kidney fat excluded)*

		Dependent variate (weight of fat in g.)— <i>Y</i>				
Population	No. of pairs	Measurement Independent variate = <i>X</i>	Correlation coeff.	<i>P</i>	Regression coeff. <i>r</i> , <i>X</i>	Regression equation
Lambs	11	<i>C</i>	0.7023	<0.02	537.87	$Y = 537.87X + 2596$
	11	<i>J</i>	0.8244	<0.01	231.2	$Y = 231.2X + 2194$
	11	<i>Y</i>	0.723	<0.02	—	—
	11	$C + J + Y$	0.8084	<0.01	136.3	$Y = 136.3X + 2123$
	11	$\frac{L+F}{10} \times \frac{C+J+Y}{3}$	0.7809	<0.01	5.691	$Y = 5.691X + 1765$
	11	$\frac{L}{10} \times (C + J + Y)$	0.7912	<0.01	2.577	$Y = 2.577X + 1907$
Hoggets	5	<i>C</i>	0.9435	<0.02	509.2	$Y = 509.2X + 4900$
	5	<i>J</i>	0.8227	>0.05	—	—
	5	<i>Y</i>	0.893	<0.05	297.7	$Y = 297.7X + 5184$
	5	$C + J + Y$	0.947	<0.02	123.75	$Y = 123.75X + 4233$
	5	$\frac{L+F}{10} \times \frac{C+J+Y}{3}$	0.9467	<0.02	4.307	$Y = 4.307X + 4008$
	5	$\frac{L}{10} \times (C + J + Y)$	0.9538	<0.01	2.021	$Y = 2.021X + 4046$
Within ages	16	<i>C</i>	—	—	522.56	—
	16	$C + J + Y$	—	—	129.41	—
	16	$\frac{L}{10} \times (C + J + Y)$	—	—	2.262	—
Dependent variate (weight of fat as percentage of bone weight) —						
Lambs	11	<i>F</i>	—0.7446	<0.01	—1.95	
Hoggets	5	<i>F</i>	—0.8514	<0.1	—2.604	

D. MEASUREMENTS AS INDICES OF QUALITY AS AFFECTED

BY CONFORMATION

(1) *External measurements*

As referred to above the value of an animal for meat depends on its conformation as well as on its composition. Various external carcass measurements, though not correlated with the composition of the carcass, are useful measures of its conformation. The leg length *F* should be absolutely short—for reasons already given. The width and depth of gigots (*G* and *H*), as well as measurement *I*, give an idea of the fullness of the thighs and should be large. Unfortunately these measurements may be affected by the skeletal framework as well as the fleshiness in this region. The best picture of the compactness of the hind-quarters is provided by the ratio of width of gigots to leg length (*G/F*). The higher this ratio the shorter the leg relative to the thickness of the thighs.

Some of the most valuable muscles of the body run along the vertebral column on each side from the pelvis to the shoulders. This part of the carcass is usually sold in cutlets. The butcher requires as many cutlets as possible from a carcass, so the longer it is, the better. *L*—the length of body from the symphysis pubis to the first rib—gives a good measure of the length of this part. At a constant weight, increased length of body is only advantageous provided it has not been followed by reduction in muscle thickness. Therefore an increase in body length should be accompanied by reduction in weight of the neck and extremities as well as the depth of the chest.

K, the length from the tail-head to the base of the neck, cannot be taken with the same degree of accuracy as *L*, but it can be used as a substitute for the latter in cases where *L* cannot be measured, as in frozen carcasses of fat animals.

The neck and breast are cheap joints, so that a short neck (*N*) and shallow thorax (*Th*) are required.

(2) *Measurements of muscular development at the last rib as indices to carcass quality*

An ideal cutlet has a large deep "eye muscle", elliptical to circular in shape, the upper level of which should reach above the point of the spinous process. Such a cutlet is more attractive and has more muscle in proportion to bone than one with an oblong, shallow muscle with the spinous process standing far above its upper level. The latter cutlet is inclined to dry on cooking, while the former will remain juicy.

The greater the depth *B* in proportion to the length *A*¹ the better. Hammond (1936) and Hirzel (1936) have calculated *B* as a percentage of *A* and given it the term "Shape Index". Hirzel (1936) found that prize-winners and champions in the carcass classes at the Smithfield Show had a higher Shape Index than those which were not awarded a prize. A good development of muscle on the lower half of the rib is a desirable character. When a carcass is sufficiently fat on the loin and the legs it is usually excessively fat on the sternum and lower part of the ribs. Thick muscular layers on the ribs thus increase greatly the value of this part.

¹ The measurement *A* which is here referred to as length of eye muscle (*longissimus dorsi*) is more correctly called "width" of eye muscle. However, to avoid confusion we continue to refer to it as length of eye muscle as previous workers (Hammond and Hirzel) have done.

(3) *Development of fat at the last rib as an index of quality*

Of the tissues fat is the most important factor in determining carcass quality at any given weight (Hirzel, 1936).

Absolute fat measures on the loin cut thus assume considerable significance. Deficiency in fatness is most easily observed at *G*, while at *J* excessive fat is inclined to accumulate. Hirzel found that the optimum thickness of fat at *C*, which he considered the most important measure, was 6.5-7.0 mm. during the years 1927-32 for carcasses of 9-21 months old. Any excess in *C* over 9 mm. was followed by a reduction in price per lb. of the carcass. It is desirable that the ratio *J/C* should remain low, as that indicates little danger of over-fatness (patchiness) on the ribs.

The value of measurement *J* was not studied by Hirzel. We believe this to be a much more important measurement from the quality point of view than *Y*. A drawback with both *X* and *Y* is that it is difficult always to record them at the same point.

(4) *The cannon bone as an index of carcass quality*

It was obvious, from the data of the dissected animals (Part III), that the short-boned individuals had a higher Shape Index of "eye muscle" than the long-boned. This suggested the possibility of a correlation between the length of the fore-cannon and the Shape Index, using data from sheep referred to in Part II.

As shown in Table 5 the relationship between these variates has been calculated for lambs of different breeds at 33-40 and 41-48 lb. re-

Table 5. *Correlation between Shape Index of "eye muscle" and length of the fore-cannon*

Population	No. of pairs	Dependent variate <i>Y</i>	Independent variate <i>X</i>	Correlation coeff.	<i>P</i>	Regression coeff. <i>Y</i> , <i>X</i>	Regression equation
Lambs:							
33-40 lb.							
Southdown x B.L.-Chev.	23	$B/A \times 100$	Length of left fore-cannon	-0.1589	>0.05	—	—
B.L. x Blackfaced	14	"	"	-0.0737	>0.05	—	—
Blackfaced	9	"	"	-0.0685	>0.05	—	—
Different breeds	57	"	"	-0.5792	<0.01	-0.583	$Y = 118.5 - 0.583X$
Lambs:							
41-46 lb.							
Southdown x B.L.-Chev.	12	"	"	-0.2775	>0.05	—	—
Suffolk x B.L.-Chev.	8	"	"	-0.5690	>0.05	—	—
Oxford x B.L.-Chev.	20	"	"	-0.3767	>0.05	—	—
Different breeds	58	"	"	-0.6470	<0.01	-0.638	$Y = 129.4 - 0.638X$
Hoggets:							
57-64 lb.							
Oxford x B.L. Chev.	20	"	"	-0.6162	<0.01	—	—

spectively, and for Oxford \times Border Leicester-Cheviot hoggets at 57–64 lb. carcass weight. In all cases there is a negative correlation between the Shape Index and the cannon-bone length. Within each breed in the lambs these correlations are not significant, but when the breeds are lumped, the correlation is highly significant at the 1 % level. This is also the case within breeds in the hoggets.

This shows that at a constant weight there is a trend for short-boned animals to have absolutely deep “eye muscle” relative to their length Δ . This is, however, more marked between breeds than within any one breed, viz. long-legged breeds have poorer Shape Index of eye muscle than short-boned ones.

§ II. THE VALUE OF “SAMPLE JOINTS” FOR ESTIMATING COMPOSITION OF THE CARCASS

It would be a great advantage to be able to obtain an estimate of the weight of bone, muscle and fat in the carcass from one or more “sample joints”, as the expense and labour required for dissecting the whole carcass are great.

When selecting a suitable sample joint the following precautions must be considered.

The joint should be as far as possible typical of the whole carcass in its rate of development. It should not be liable to great cutting errors in jointing. Preferably a sample joint should be from a valuable part of the body, as it is of less importance to acquire exact information about the composition of a cheap cut. For that reason the neck and thorax are unsuitable. The shoulders are probably the best from the point of view of composition, but they are liable to jointing errors. The latter is also true of the pelvis, which has three cut surfaces. The leg and the loin can be cut with the greatest precision. Since, in addition, they are valuable and relatively easy to dissect accurately, they are best suited for the purpose we have in mind. If a single joint is used the leg will be the best. However, due to its relatively early development and small amount of fat, its use may cause slight underestimation of total body fat in early maturing over-fat animals.

The loin, on the other hand, is a late-developing joint in which much fat is accumulated later in life. Therefore the use of one leg + loin is likely to give more satisfactory results than the use of either of these joints alone. The relationship between the constituents of each joint, both separately and in combination, and the same constituents of the total carcass are given in Tables 6–8.

The leg. There is a very high correlation between the weight of all the constituents of the leg and the same constituents of the total carcass both in the case of lambs and hoggets (Tables 6-8). The reason for this is explained above. It appears that a quite satisfactory estimate of the carcass composition of lambs and hoggets can be made from one leg as a sample joint by the use of the regression equations developed for the purpose.

The loin. In the hoggets the loin is quite as satisfactory as the leg for estimating the total composition (Tables 6-8). This confirms the opinion that a late developing part gives a better estimate of the total carcass of more mature animals than an early developing one. The suitability of the loin in the case of the lambs is penalized by the variable number of vertebrae unfortunately characteristic of this joint; this imposes a limitation upon its use for the purpose of estimation, which is only partially overcome by attempts to correct for the variable vertebral number. Thus in bone, correction by use of the factors $\frac{9}{7}$ and $\frac{6}{5}$ to bring each to a common basis of 6 considerably improves the correlation between loin, bone, and total bone, $r = 0.9465$ as compared with $r = 0.8770$ in the uncorrected data.

When weight of muscle and fat was corrected in the same way, lower correlations were obtained. In Tables 7 and 8 the correlations for muscle and fat from the uncorrected weights are given. These are satisfactory, although in the case of muscle r is lower than for the leg.

This condition can only be explained by the fact that with an increase in the number of vertebrae we get an increase in all tissue, but proportionately greater in bone than muscle and fat.

With an increase in age and weight the proportions of muscle and fat to bone in the long loins (7 lumbar) would most likely approach the proportions in normal loins.

Table 6. *Correlation between weight of bones in sample joints and weight of bones in carcass (head and feet excluded)*

Dependent variate (bone in carcass, g.) = Y						
Population	No. of pairs	Independent variate = X	Correlation coeff.	P	Regression coeff. Y, X	Regression equation
Lambs	11	Bone in 1 leg (g.)	0.9514	<0.01	6.935	$Y = 6.935X + 420.7$
	11	Bone in loin (g.)	0.8770	<0.01	7.21	$Y = 7.21X + 1086$
	11	Bone in 1 leg + loin (g.)	0.9727	<0.01	4.00	$Y = 4X + 510$
Hoggets	5	Bone in 1 leg (g.)	0.9612	<0.01	7.59	$Y = 7.59X + 526$
	5	Bone in loin (g.)	0.9731	<0.01	11.42	$Y = 11.42X + 743$
	5	Bone in 1 leg + loin (g.)	0.9816	<0.01	4.70	$Y = 4.70X + 533$
Within ages	16	Bone in 1 leg (g.)	0.9542	<0.01	7.154	—
	16	Bone in loin (g.)	0.8934	<0.01	8.158	—
	16	Bone in 1 leg + loin (g.)	0.9732	<0.01	4.21	—

Table 7. *Correlation between weight of muscle in sample joints and weight of muscle in carcass (head and feet excluded)*

Population	No. of pairs	Independent variate = X	Dependent variate (weight of muscle in carcass, g.) = Y			
			Correlation coeff.	P	Regression coeff. Y, X	Regression equation
Lambs	11	Muscle in 1 leg (g.)	0.8965	<0.01	8.75	$Y = 8.75 X - 1971$
	11	Muscle in loin (g.)	0.8369	<0.01	3.44	$Y = 3.44 X + 5357$
	11	Muscle in 1 leg + loin (g.)	0.9187	<0.01	2.86	$Y = 2.86 X + 2350$
Hoggets	5	Muscle in 1 leg (g.)	0.9153	<0.05	5.80	$Y = 5.80 X + 3477$
	5	Muscle in loin (g.)	0.8852	<0.05	6.15	$Y = 6.15 X + 3925$
	5	Muscle in 1 leg + loin (g.)	0.9835	<0.01	3.58	$Y = 3.58 X + 1613$
Correlation within ages						
Lambs and hoggets	16	Muscle in 1 leg (g.)	0.8861	<0.01	6.482	—
	16	Muscle in loin (g.)	0.8274	<0.01	4.02	—
	16	Muscle in 1 leg + loin (g.)	0.9427	<0.01	3.1204	—

Table 8. *Correlation between weight of fat in sample joints and weight of fat in carcass (head and feet and kidney fat excluded)*

Population	No. of pairs	Independent variate = X	Dependent variate (weight of fat in carcass, g.) = Y			
			Correlation coeff.	P	Regression coeff. Y, X	Regression equation
Lambs	11	Fat in 1 leg (g.)	0.9505	<0.01	9.976	$Y = 9.976 X + 1428$
	11	Fat in loin (g.)	0.9417	<0.01	7.23	$Y = 7.23 X + 30$
	11	Fat in 1 leg + loin (g.)	0.9708	<0.01	4.42	$Y = 4.42 X + 406$
Hoggets	5	Fat in 1 leg (g.)	0.9042	<0.05	18.57	$Y = 18.57 X - 1501$
	5	Fat in loin (g.)	0.9644	<0.01	3.33	$Y = 3.33 X + 4090$
	5	Fat in 1 leg + loin (g.)	0.9775	<0.01	2.95	$Y = 2.95 X + 3053$
Correlation within ages						
Lambs and hoggets	16	Fat in 1 leg (g.)	0.9043	<0.01	11.058	—
	16	Fat in loin (g.)	0.8833	<0.01	4.38	—
	16	Fat in 1 leg + loin (g.)	0.9540	<0.01	3.606	—

Leg + loin. The correlation between the weight of bone in one leg + loin and the weight of bone in the carcass approaches unity, both in the case of lambs and hoggets, though no correction has been made for irregularity in the number of lumbar vertebrae in the lambs. The data indicate that still more accurate estimates of the weight of the total skeleton can be obtained by the use of the regressions for leg + loin than from either alone.

A similar situation exists in respect to muscle though the difference is but little in lambs.

In fat the combined joints provide a much more reliable basis than the leg alone.

Further data are required to enable one to calculate separately the regression of the weight of any constituent in the loin on the weight of the same constituent in the whole carcass for sheep with 6 and with 7 lumbar

vertebrae. Until that can be done one is liable to cause some error in estimating the composition of the body from that of the loin, which, however, otherwise appears to be a good sample joint.

SUMMARY

1. By establishing the relationship between linear carcass measurements and the quantitative composition of the carcass in terms of bone, muscle and fat, we have provided a scientific basis for the use of many measurements hitherto only presumed to provide an index to carcass quality.

2. External carcass measurements are correlated with weight of the skeleton. The most useful for this purpose are length of tibia + tarsus and length of the fore-cannon.

3. As indices of muscle, external measures are only of indirect value. Thus, both $F - T$ and $G/F \times 100$ are strongly correlated with weight of muscle as a percentage of skeletal weight.

4. Similarly, F provides an index of fat, being negatively correlated with fat as a percentage of bone.

5. For muscle and fat internal measures permit a more precise estimate to be made. $A + B$ is the best index of the former while $C + J + Y$ provide the most accurate estimate of the weight of fat.

6. Still better indices for muscle and fat are provided by suitable combinations of external and internal measurements. Thus $L/10 + A + B$ is very highly correlated with the weight of muscle, and $L/10 \times (C + J + Y)$ is the best index of fat in the hoggets. For bone, a most efficient single index is shown to be the weight of the fore-cannon bone.

7. The weight of the skeleton can be estimated with a high degree of accuracy from the weight of the bones in either one leg or loin. Both these joints combined, however, provide a still better estimate.

8. The muscle in one leg or loin + leg provides an excellent index of the weight of muscle in the whole carcass.

9. The fat in one leg, loin, or both these joints combined provides a good index of the weight of the total fat in the carcass. Both joints combined give the most precise measure.

10. The value of certain measurements which are not necessarily associated with the quantity of the major tissues of the carcass, but which nevertheless have important qualitative significance, is emphasized.

PART II. COMPARATIVE STUDY OF DIFFERENT BREEDS AND CROSSES

INTRODUCTION

With the present demand for lamb of certain weights and high quality, and the keen competition in the world's meat market, it is of vital importance that the practical sheep farmer should use those breeds which are best suited for the production of the required article. Those producing inferior quality are more likely to lose hold in the markets, particularly in times of over-production and low prices.

It is recognized that the farmer has to consider various factors besides the mutton qualities of his sheep. This is particularly the case with the ewe flock. Natural conditions often limit the choice to a certain local breed. The relative importance of wool and meat, the prolificacy of the breed and the milking qualities of the ewes are also factors which must receive careful attention. The farmer can, however, by the use of a suitable ram do much to improve the meat qualities of the lambs, even when his ewe flock is necessarily of a type not particularly suited for quality meat production. Experience has shown, for example, that the New Zealand farmer can produce the most favoured fat lambs of to-day by using the Southdown ram on the Romney ewe, which is relatively unimproved from meat quality point of view, and which is bred mainly for its wool.

At present there is little reliable practical or experimental evidence on the comparative value of different breeds of sheep for meat production. Hirzel (1936) has compared several British breeds in respect of mutton qualities. His material, however, consisted of show animals, and his observations in consequence are likely to have given greater merit to certain breeds than warranted by their performance under practical conditions. Also, his work does not directly elucidate the value of the various breeds for fat lamb production, as all the animals were approximately 9 or 21 months old. Sheep-crossing experiments on fat lamb production have been carried out over a five-year period at Leeds University (Robertson, 1936). Unfortunately these do not demonstrate conclusively the effect of breed on the carcass qualities of the offspring, as the financial return per ewe was taken as a basis of comparison. The latter is affected by number of lambs born in each lot as well as by fluctuations in meat prices. Only in the last year of these experiments were the lambs graded under the Ministry of Agriculture Grade and

Dead Weight system of marketing, and accordingly they have some relation to market suitability.

The object of the present investigation is to make a comparative study of various Scottish breeds and crosses based on carcass quality measurements. For comparative purposes data on the English Suffolk and the native Iceland breed and its cross with the Border Leicester have also been incorporated in this study. By this we hope to throw light on the relative merits of the different breeds and crosses in respect of their meat qualities, both for lamb and mutton production.

MATERIAL AND METHODS

A general account of the material used has already been given (p. 549).

Numbers of carcasses of lambs and hoggets of the various breeds enumerated were measured and weighed, as previously described. The number of individuals of each breed studied and the mean weights and measurements for each weight class are given in Appendices VI and VII. Though large numbers of individuals have been studied, animals of each breed are distributed over large weight ranges. This accounts for the fact that in many weight classes only few individuals occur. In the beginning of the investigation it was decided to study animals of each breed both as lambs and as hoggets, to obtain a measure of the age changes within any one breed, as well as the relative merits of each breed for lamb and mutton production. Unfortunately, only four of the breeds were available for study at both ages. It was impossible to obtain data on the Blackfaced and Southdown \times B.L.-Cheviot hoggets. The latter is a cross for fat-lamb raising and is not popular for hoggeting. On the other hand, Blackfaces are fattened in large numbers in the Lowlands in winter and sold fat as hoggets. Though these are popular in the Edinburgh fat stock markets in winter they are, with very few exceptions, bought by London buyers, who readily overbid the local butchers. This illustrates the relatively greater demand for the small joints in London and other large cities as compared with Scotland.

Similar difficulty was met with in respect of the lambs. No data on Cheviot lambs could be obtained and very few Blackfaced lambs were available for study.

It will be noticed that there is considerable irregularity in the number of individuals of each breed falling in any one weight class. This is mainly due to breed differences. From the point of view of applying statistical methods to the data this adds to the difficulty, but it gives

valuable information about the weights at which animals of the different breeds become ready for slaughter. Since these are all commercial animals they are not sold to the butcher until they have attained marketable quality. This explains why lambs of some of the large breeds, i.e. Suffolk \times Border Leicester-Cheviot and Border Leicester-Cheviot, of less than 40 lb. dressed carcass were not met with, while large numbers of lambs of the smaller breeds such as Southdown \times B.L.-Cheviot and B.L. \times Blackfaced were frequent under this weight.

Weight and external measurements of large numbers of carcasses were recorded. Due to various reasons only some could be cut through at the last rib and the development of the muscle and fat in that region measured. In view of the fact that the external measurements alone are of much less value for estimating the carcass quality than those taken on the cut surface at the last rib, carcasses of which only external measurements were available have not been included in this work. Only wethers have been used for breed comparison, to eliminate the effect of sex. This results in there being very few representatives of the Iceland and B.L. \times Iceland breeds included in the statistical comparison, as it is not a general practice to castrate ram lambs in that country, and most of the available data on these breeds are from entire ram lambs or females. Data on these as well as on a few females of other breeds are given in Appendix VII. That the few Iceland and B.L. \times Iceland wether lambs can be considered fairly typical of these breeds is clear by comparing their measurements with those of the ram lambs (Appendix VII).

The left fore-cannon bone of each sheep was collected for a special study. It was cleaned by removing completely any tendons adhering to it and weighed immediately afterwards.

Lambs and hoggets of each breed were respectively grouped in weight classes of 8 lb. dressed cold carcass weight, i.e. 25-32, 33-40 lb., etc. The average of those measurements, which are of greatest value as indices of carcass quality, for each weight class (Part I), have been graphed to illustrate the breed differences. The changes in the measurements with an increase in age and weight are also elucidated in these diagrams.

The breeds were compared at constant weight. Due to the excessive work involved in ascertaining the significance of differences between breeds at all weights, it was decided to analyse the data statistically only for those weight classes where all the breeds were represented in reasonably large numbers.

The magnitude of the breed differences in all weight classes is shown in the diagrams and the tables. Since the significance of these differences

has been calculated for one or more weight classes at both ages, one can see from the diagrams whether the general trend is the same at other weights. Another justification for not calculating the significance of breed differences at all weights is the fact that at the extreme weights only few breeds are represented and usually by small numbers of individuals. Two weight classes of lambs—33–40 lb. and 41–48 lb.—were analysed, because in no one weight class were all the breeds represented. The hoggets were compared at 60 lb. (weight class 57–64 lb.).

Fisher's method of analysis of variance was used. To ascertain whether variation between breed means was significantly greater than that within breeds Snedecor's F —here equal to the ratio mean square between breeds : mean square within breeds—was used. Where the individual variances calculated for each breed did not differ significantly and the F test was significant at either 1 or 5% level, the standard error per sheep was calculated from the pooled sum of squares within breeds for each measurement. The significance of the difference between any two breeds was tested by T , using the variance from the analysis of variance table. In cases where there was a significant inhomogeneity between the individual breed variances, breed averages were compared by the ordinary T test.

Large numbers of the cannon bones have been photographed to illustrate the effect of breed at constant weight and changes due to weight increase on the shape of the bones. Where the total number of cannon bones from a weight class was not photographed the following precautions were taken to ensure that those which were photographed were typical for the weight class in question. They were arranged in order of increased length and every second bone picked out until sufficiently small numbers were left. The shortest and the longest bones were always photographed to illustrate the maximum variation in each weight class.

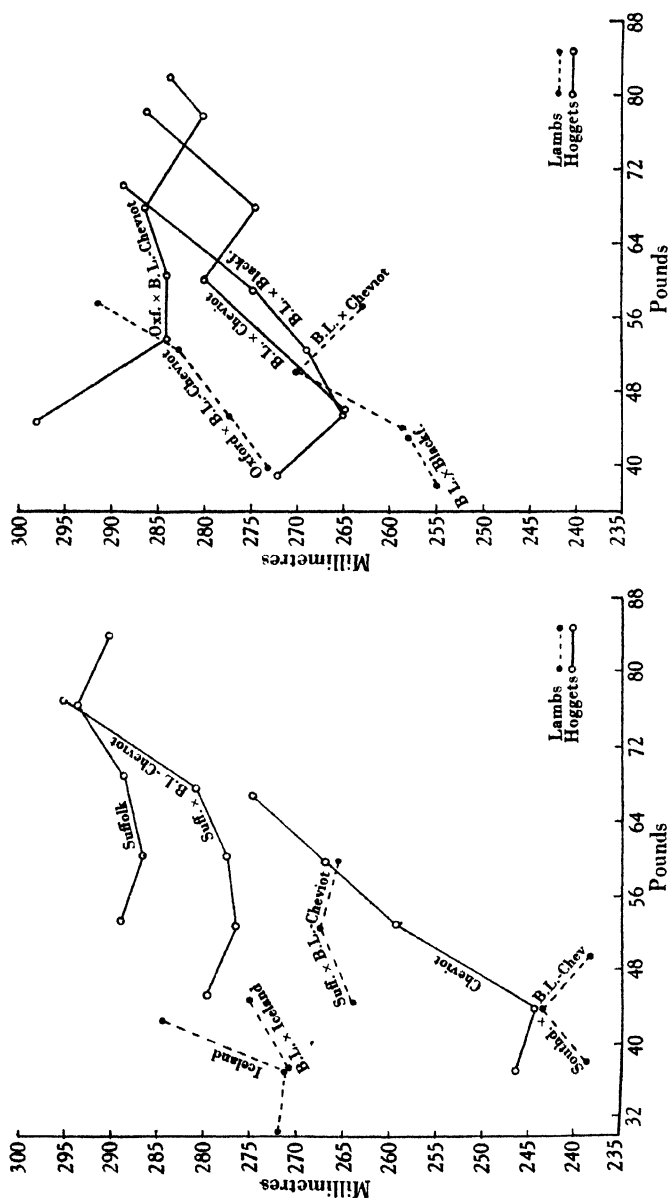
§ I. COMPARISON OF THE DIFFERENT BREEDS AS LAMBS (4–5 MONTHS OLD)

A. BREED DIFFERENCES AT CONSTANT WEIGHT

(1) *External measurements (carcass conformation)*

(a) *Length of leg P and length of tibia + tarsus T.*

The length of leg and tibia + tarsus and combinations of these are, as demonstrated in Part I, the most important external carcass measurements, as indices of the conformation and quality. Tables 9 and 10

Text-fig. 2. Changes with breed, age and weight. Leg length (*F*).

show the average leg length in lambs of the different breeds at 33-40 and 41-48 lb., standard errors, and the significance of the breed differences. Breed differences are highly significant. At 33-40 lb. the Southdown \times B.L.-Cheviot and the Blackfaced have the shortest legs. The B.L. \times Blackfaced is in an intermediate position, the Iceland, B.L. \times Iceland and Oxford \times B.L.-Cheviot have approximately the same leg length but longer legs than the other breeds. At 41-48 lb. no Blackfaced occur, while Suffolk \times B.L.-Cheviot and B.L. \times Cheviot are represented. The general trend is the same as at 33-40 lb.; Southdown \times B.L.-Cheviot has the shortest leg, the B.L. \times Blackfaced, B.L. \times Cheviot and Suffolk \times B.L.-Cheviot are intermediate and do not themselves differ significantly. The B.L. \times Iceland, Oxford \times B.L.-Cheviot and Iceland have longer legs than the other breeds (Text-fig. 2).

Tables 11 and 12 show that the order of merit is the same in respect of *T*. The Iceland and B.L. \times Iceland have longer tibias than the Oxford \times B.L.-Cheviot, though not significantly so at 33-40 lb. The B.L. \times Blackfaced has slightly shorter *T* than the B.L. \times Cheviot (Text-fig. 3).

Table 9. *Significance of breed differences*

Lambs: 33-40 lb. carcass weight. Leg length (*F*).

$F=13.11$ S. Standard error per sheep = 5.1% of mean.

Average mm.	Iceland	B.L. \times Iceland	Black- faced	B.L. \times Black- faced	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	s.e. of mean	No. of in- dividuals
Iceland	271.0	N.S.	S.	s.	S.	N.S.	5.674	5
B.L. \times Iceland	N.S.	271.0	S.	s.	S.	N.S.	6.344	4
Blackfaced	S.	S.	239.555	S.	N.S.	S.	4.229	9
B.L. \times Blackfaced	s.	s.	S.	255.066	S.	s.	3.276	15
Southdown \times B.L.-Chev.	S.	S.	N.S.	S.	238.391	S.	2.646	23
Oxford \times B.L.-Chev.	N.S.	N.S.	S.	s.	S.	273.0	6.344	4

S. = significant $P=0.01$. s. = significant $P=0.05$. N.S. = not significant.

Table 10. *Significance of breed differences*

Lambs: 41-48 lb. carcass weight. Leg length (*F*).

$F=13.46$ S. Standard error per sheep = 4.3% of mean.

Average mm.	Iceland	B.L. \times Iceland	B.L. \times Black- faced	B.L. \times Chev	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	Suffolk \times B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	284.333	N.S.	S.	S.	S.	N.S.	s.	6.645	3
B.L. \times Iceland	N.S.	275.0	s.	s.	S.	N.S.	N.S.	5.147	5
B.L. \times Blackfaced	S.	s.	258.0	N.S.	S.	S.	N.S.	4.069	8
B.L. \times Chev.	S.	s.	N.S.	258.5	s.	S.	N.S.	5.755	4
Southdown \times B.L.-Chev.	S.	S.	S.	s.	243.667	S.	S.	3.3226	12
Oxford \times B.L.-Chev.	N.S.	N.S.	S.	S.	S.	277.35	S.	2.574	20
Suffolk \times B.L.-Chev.	s.	N.S.	N.S.	N.S.	S.	S.	264.111	3.8365	9

S. = significant $P=0.01$. s. = significant $P=0.05$. N.S. = not significant.

Table 11. *Significance of breed differences*

Lambs: 33-40 lb. carcass weight. Length of tibia and tarsus (T).

 $F=21.50$ S. Standard error per sheep = 3.4 % of mean.

Average mm.	Iceland	B.L. × Iceland	Black- faced	B.L. × Black- faced	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	207.8	N.S.	S.	S.	S.	N.S.	2.921	5
B.L. × Iceland	N.S.	209	S.	S.	S.	N.S.	3.266	4
Blackfaced	S.	S.	183.888	S.	N.S.	S.	2.177	9
B.L. × Blackfaced	S.	S.	S.	193.333	S.	S.	1.686	15
Southdown × B.L.-Chev.	S.	S.	N.S.	S.	185.695	S.	1.362	23
Oxford × B.L.-Chev.	N.S.	N.S.	S.	S.	S.	204.75	3.266	4

S. = significant $P=0.01$. s. = significant $P=0.05$. N.S. = not significant.Table 12. *Significance of breed differences*

Lambs. 41-48 lb. carcass weight. Length of tibia and tarsus (T).

 $F=14.67$ S. Standard error per sheep = 3.5 % of mean.

Average mm.	Iceland	B.L. × Iceland	B.L. × Black- faced	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	219.00	N.S.	S.	S.	S.	s	S.	4.146	3
B.L. × Iceland	N.S.	217.80	S.	S.	S.	S.	S.	3.212	5
B.L. × Blackfaced	S.	S.	197.625	N.S.	s.	S.	N.S.	2.539	8
B.L. × Chev.	S.	S.	N.S.	203.00	S.	N.S.	N.S.	3.591	4
Southdown × B.L.-Chev.	S.	S.	s.	S.	190.25	S.	S.	2.073	12
Oxford × B.L.-Chev.	s.	S.	S.	N.S.	S.	208.05	N.S.	1.606	20
Suffolk × B.L.-Chev.	S.	S.	N.S.	N.S.	S.	N.S.	203.78	2.394	9

S. = significant at 1 %. s. = significant at 5 %. N.S. = not significant.

The difference between F and T ($F-T$) in lambs of the various breeds is given in Table 13. The smaller this difference the greater is the proportion of muscle to bone. The Southdown × B.L.-Cheviot is the best, followed by the Blackfaced at 33-40 lb. and the Suffolk × B.L.-Cheviot at 41-48 lb. The Oxford × B.L.-Cheviot is the poorest at all weights. This agrees with the results from the dissected lambs of these breeds (Part III).

Table 13. *Difference between leg length and length of tibia + tarsus ($F-T$) in mm. in lambs*

Breed	Weight classes (lb.)				
	25-32	33-40	41-48	49-56	57-64
Iceland	73.0	63.2	65.3	—	—
B.L. × Iceland	—	62.0	57.2	—	—
Blackfaced	—	55.7	—	—	—
B.L. × Blackfaced	—	62.0	60.4	—	—
B.L. × Chev.	—	—	55.5	61.1	54.7
Southdown × B.L.-Chev.	—	52.7	53.4	44.0	—
Oxford × B.L.-Chev.	—	70.3	69.3	68.5	63.8
Suffolk × B.L.-Chev.	—	—	60.3	55.0	54.4

(b) *Width and depth of gigots (G and H).*

These measurements, though not directly correlated with carcass composition, are an indication of the development of the hindquarters. At 33-40 lb. the breeds do not differ significantly in *G*, but the Oxford × B.L.-Cheviot has significantly greater *H* than the other breeds (Table 14). This can, however, be due to the very coarse frame of this cross.

Table 14. *Significance of breed differences*Lambs: 33-40 lb. carcass weight. Depth of gigots (*H*). $F=3.36$ s. Standard error per sheep = 5.2 % of mean.

Average mm.	Iceland	B.L. × Iceland	Black- faced	B.L. × Black- faced	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	120.8	N.S.	N.S.	N.S.	N.S.	S.	2.902	5
B.L. × Iceland	N.S.	119.75	N.S.	N.S.	N.S.	S.	3.244	4
Blackfaced	N.S.	N.S.	122.444	N.S.	N.S.	S.	2.163	9
B.L. × Blackfaced	N.S.	N.S.	N.S.	126.406	N.S.	N.S.	1.675	15
Southdown × B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	126.304	s.	1.353	23
Oxford × B.L.-Chev.	S.	S.	S.	N.S.	s.	133.5	3.244	4

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

Table 15. *Significance of breed differences*Lambs: 41-48 lb. carcass weight. Width of gigots (*G*). $F=3.31$ S. Standard error per sheep = 3.1 % of mean.

Average mm.	Iceland	B.L. × Iceland	B.L. × Black- faced	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	228.333	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	4.154	3
B.L. × Iceland	N.S.	231.4	N.S.	N.S.	N.S.	N.S.	N.S.	3.218	5
B.L. × Blackfaced	N.S.	N.S.	226.875	N.S.	S.	S.	S.	2.544	8
B.L. × Chev.	N.S.	N.S.	N.S.	225.0	S.	s.	s.	3.598	4
Southdown × B.L.-Chev.	N.S.	N.S.	S.	S.	237.08	N.S.	N.S.	2.077	12
Oxford × B.L.-Chev.	N.S.	N.S.	S.	s.	N.S.	235.0	N.S.	1.609	20
Suffolk × B.L.-Chev.	N.S.	N.S.	S.	S.	N.S.	N.S.	236.607	2.3984	9

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

Table 15 shows that at 41-48 lb. the B.L. × Blackfaced and B.L. × Cheviot have less width of gigots than the other breeds, which do not differ significantly. The Southdown, Suffolk and Oxford crosses with the B.L. × Cheviot have similar depth of gigots and are deeper than the Iceland, B.L. × Iceland and B.L. × Cheviot (Table 16). The B.L. × Blackfaced is intermediate.

The shape of the hindquarters as measured by $(G/F \times 100)$ varies much with breed (Table 40). The Southdown × B.L.-Cheviot is of outstanding merit in this respect. At 49-56 lb. the width of gigots is greater than the leg length, which can be considered excellent. The Blackfaced and Suffolk × B.L.-Cheviot, followed by the B.L. × Blackfaced, have poorer

shaped hindquarters, while the Iceland, Oxford × B.L.-Cheviot and B.L. × Iceland are poorest.

(c) *Length of body L.*

The breed differences as measured by *L* (the distance from the symphysis pubis to the first rib) are illustrated in Tables 17 and 18 for

Table 16. *Significance of breed differences*

Lambs: 41-48 lb. carcass weight. Depth of gigots (*H*).

$F=5.55$ S. Standard error per sheep = 5.9% of mean.

Average mm.	Iceland	B.L. × Iceland	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	122.67	N.S.	N.S.	S.	S.	S.	4.566	3
B.L. × Iceland	N.S.	126.0	N.S.	S.	S.	S.	3.537	5
B.L. × Chev.	N.S.	N.S.	124.75	S.	S.	S.	3.955	4
Southdown × B.L.-Chev.	S.	S.	S.	137.50	N.S.	N.S.	2.283	12
Oxford × B.L.-Chev.	S.	S.	S.	N.S.	138.50	N.S.	1.769	20
Suffolk × B.L.-Chev.	S.	S.	S.	N.S.	N.S.	138.89	2.636	9

S. = significant at 1%. s. = significant at 5%. N.S. = not significant.

N.B. Data on this measurement for the B.L. × Blackfaced were not homogeneous with the data for the other breeds. The mean 134.375 with s.e. 0.3906 is significantly greater than the means of Iceland, B.L. × Iceland, B.L. × Cheviot and less than Oxford × B.L.-Cheviot (using simple *t* test).

Table 17. *Significance of breed differences*

Lambs: 33-40 lb. carcass weight. Length of body (*L*).

$F=10.72$ S. Standard error per sheep = 3.1% of mean.

Average mm.	Iceland	B.L. × Iceland	Black- faced	B.L. × Black- faced	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	578.0	s.	N.S.	N.S.	s.	N.S.	8.015	5
B.L. × Iceland	s.	602.5	S.	N.S.	S.	N.S.	8.961	4
Blackfaced	N.S.	S.	562	S.	N.S.	S.	5.974	9
B.L. × Blackfaced	N.S.	N.S.	S.	586.667	S.	N.S.	4.6.8	15
Southdown × B.L.-Chev.	s.	S.	N.S.	S.	554.565	S.	3.737	23
Oxford × B.L.-Chev.	N.S.	N.S.	S.	N.S.	S.	595.5	8.961	4

S = significant $P =$ s = significant $P = 0.05$. N.S. = not significant.

Table 18. *Significance of breed differences*

Lambs: 41-48 lb. carcass weight. Length of body (*L*).

$F=7.75$ S. Standard error per sheep = 2.9% of mean.

Average mm.	Iceland	B.L. × Iceland	Black- faced	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	611.667	N.S.	N.S.	N.S.	S.	N.S.	N.S.	10.117	3
B.L. × Iceland	N.S.	630.0	s.	N.S.	S.	N.S.	N.S.	7.822	5
B.L. × Blackfaced	N.S.	s.	606.75	N.S.	S.	N.S.	N.S.	6.196	8
B.L. × Chev.	N.S.	S.	N.S.	598.75	S.	N.S.	N.S.	8.762	4
Southdown × B.L.-Chev.	S.	S.	S.	S.	577.083	S.	S.	5.659	12
Oxford × B.L.-Chev.	N.S.	s.	N.S.	N.S.	S.	606.25	N.S.	3.919	20
Suffolk × B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	S.	N.S.	616.555	5.6415	

S. = significant $P = 0.01$. s. = significant $P = 0.05$. N.S. = not significant.

lambs. At the lighter weight the Southdown \times B.L.-Cheviot and the Blackfaced have the shortest body. The B.L. \times Iceland, the Oxford \times B.L.-Cheviot, and the B.L. \times Blackfaced are similar, with the longest *L*. The Iceland is shorter bodied than the B.L. \times Iceland.

At 41–48 lb. the order of merit is the same, except that the B.L. \times Iceland is significantly longer than all the other breeds with the exception of the Iceland. The difference between the last two is considerable, though not significant due to the small number.

There are two distinct causes contributing to the differences in body length. It may be due to a variation in the number of vertebrae, either thoracic or lumbar, or due to differences in the length of the vertebral bodies. In Part III the incidence of variation in number of vertebrae will be dealt with, but the incidence of animals with fourteen thoracic or seven lumbar vertebrae instead of the normal thirteen and six is more frequently met with in the large breeds and crosses than in the Mountain breeds and the Southdown crosses, which we have shown above to be shorter in body length.

(d) *Depth of thorax (Th) and length of neck (N).*

A deep thorax and a long neck are undesirable, as these are the cheapest cuts of the carcass. A high proportion of the carcass weight should not lie in these regions. Tables 19 and 20 illustrate the breed differences in the depth of thorax. The Blackfaced and Southdown \times B.L.-Cheviot have the shallowest chest at the lower weight, the Iceland and its cross with the B.L. the deepest. At the higher weight the Southdown \times B.L.-Cheviot, B.L. \times Cheviot and B.L. \times Blackfaced have a significantly shallower thorax than the other breeds, which do not differ greatly.

The Southdown \times B.L.-Cheviot and Iceland have shorter neck than the other breeds, all of which are practically identical in this measure-

Table 19. *Significance of breed differences*

Lambs: 33–40 lb. carcass weight. Depth of thorax (*Th*).

$F = 16.12$ S. Standard error per sheep = 2.8 % of mean.

Average mm.	Iceland	B.L. \times Iceland	Black- faced	B.L. \times Black- faced	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	274.6	N.S.	S.	S.	S.	s.	3.2275	5
B.L. \times Iceland	N.S.	271.75	S.	S.	S.	N.S.	3.6085	4
Blackfaced	S.	S.	248.889	S.	N.S.	S.	2.406	9
B.L. \times Blackfaced	S.	S.	S.	257.285	S.	N.S.	1.929	14
Southdown \times B.L.-Chev.	S.	S.	N.S.	S.	250.0	S.	1.505	23
Oxford \times B.L.-Chev.	s.	N.S.	S.	N.S.	S.	262.5	3.6085	

S. = significant, $P = 0.01$.

s. = significant $P = 0.05$.

N.S. = not significant.

Table 20. *Significance of breed differences*Lambs: 41-48 lb. carcass weight. Depth of thorax (*Th*). $F=9.24$ S. Standard error per sheep = 2.9% of mean.

Average mm.	Iceland	B.L. × Iceland	B.L. × Black- faced	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	277.0	N.S.	s.	S.	S.	N.S.	N.S.	4.490	3
B.L. × Iceland	N.S.	280.8	S.	S.	S.	N.S.	N.S.	3.478	5
B.L. × Blackfaced	s.	S.	284.375	N.S.	N.S.	S.	S.	2.749	8
B.L. × Chev.	S.	S.	N.S.	280.0	N.S.	S.	S.	3.888	4
Southdown × B.L.-Chev.	S.	S.	N.S.	N.S.	280.0	S.	S.	2.245	12
Oxford × B.L.-Chev.	N.S.	N.S.	S.	S.	S.	275	N.S.	1.833	18
Suffolk × B.L.-Chev.	N.S.	N.S.	S.	S.	S.	N.S.	276	2.592	9

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

Table 21. *Significance of breed differences*Lambs: 33-40 lb. carcass weight. Length of neck (*N*). $F=5.25$ S. Standard error per sheep = 11.0% of mean.

Average mm.	Iceland	B.L. × Iceland	Black- faced	B.L. × Black- faced	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	133	s.	S.	S.	N.S.	s.	7.185	5
B.L. × Iceland	s.	155	N.S.	N.S.	s.	N.S.	8.0335	4
Blackfaced	S.	N.S.	157.22	N.S.	S.	N.S.	5.366	9
B.L. × Blackfaced	S.	N.S.	N.S.	156.0	S.	N.S.	4.148	15
Southdown × B.L.-Chev.	N.S.	s.	S.	S.	135.652	s.	3.330	23
Oxford × B.L.-Chev.	s.	N.S.	N.S.	N.S.	s.	157.5	8.0335	4

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

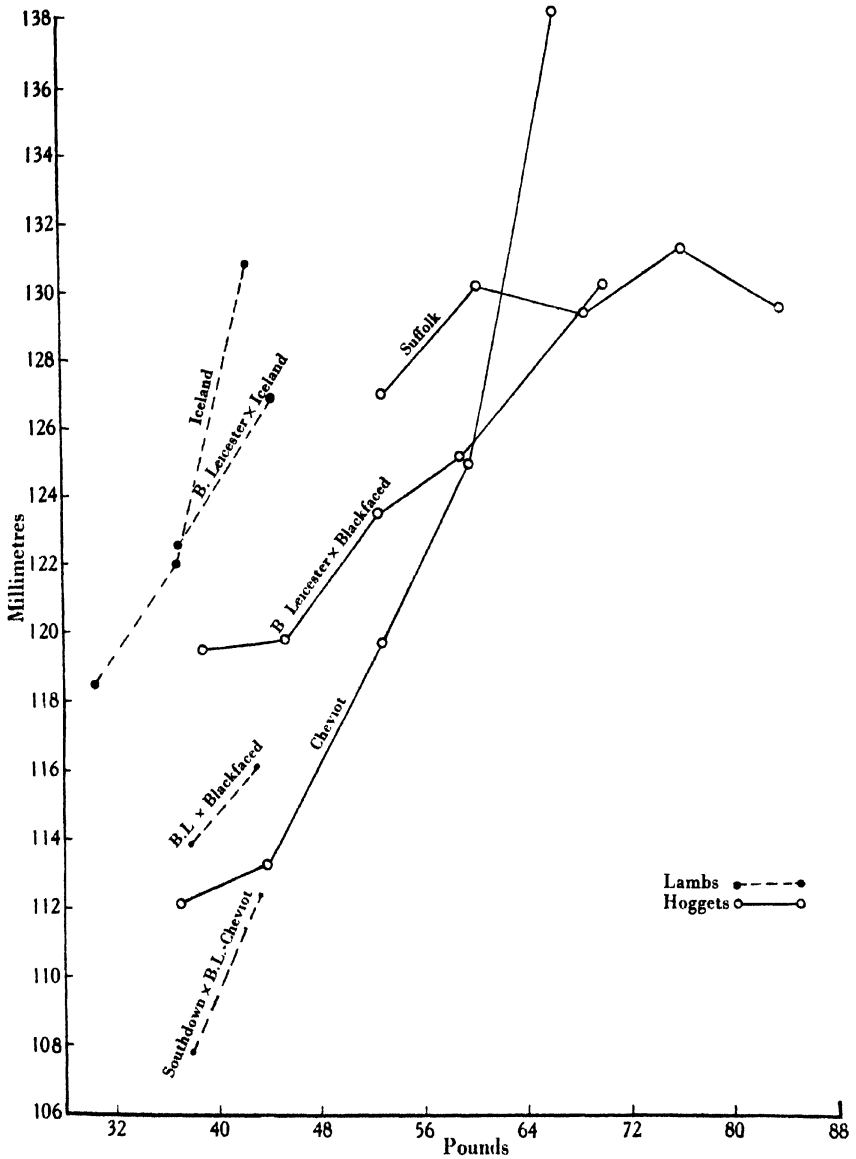
Table 22. *Significance of breed differences*Lambs: 41-48 lb. carcass weight. Length of neck (*N*). $F=10.46$ S. Standard error per sheep = 9.9% of mean.

Average mm.	Iceland	B.L. × Iceland	B.L. × Black- faced	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	143.333	N.S.	N.S.	N.S.	s.	s.	N.S.	8.699	3
B.L. × Iceland	N.S.	151.00	N.S.	N.S.	S.	N.S.	N.S.	6.738	5
B.L. × Blackfaced	N.S.	N.S.	161.875	N.S.	S.	N.S.	N.S.	5.327	8
B.L. × Chev.	N.S.	N.S.	N.S.	145.0	s.	s.	N.S.	7.534	4
Southdown × B.L.-Chev.	s.	S.	S.	s.	123.75	S.	S.	4.350	12
Oxford × B.L.-Chev.	s.	N.S.	N.S.	s.	S.	163.25	N.S.	3.309	20
Suffolk × B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	S.	N.S.	162.22	5.0225	9

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

ment (Table 21). At 41-48 lb. the Southdown cross has much shorter neck than the other breeds, followed by the Iceland and B.L. × Cheviot which, however, only differ significantly from the Oxford × B.L.-Cheviot (Table 22). The Iceland and B.L. × Iceland are not quite comparable with the other breeds in respect of this measurement, because in these two breeds the head was cut off before the neck was measured. This may cause a slight reduction in *N* due to the retraction of the neck.



Text-fig. 4. Changes with breed, age and weight. Length of cannon bone.

(2) *Cannon-bone measurements (skeletal development)*(a) *Length of left fore-cannon.*

The effect of breed on the shape of the left fore-cannon bone is illustrated in Pls. V and VI. There are great breed differences in the length of this bone. Tables 23 and 24 show the magnitude and significance of these. At both weights the Southdown \times B.L.-Cheviot have shorter cannons than the other breeds. At the lower weight, however, the Black-faced and at the higher weight the Border Leicester \times Black-faced have not significantly longer cannons (Text-fig. 4).

At 33–40 lb. the B.L. \times Black-faced is intermediate in bone length and significantly different from other breeds. The Iceland and B.L. \times Iceland have the longest cannons at both weights, though the difference is not significant when compared with the Oxford \times B.L.-Cheviot. The latter at 41–48 lb. has only slightly longer cannons than the B.L. \times Cheviot and the Suffolk \times B.L.-Cheviot, but at higher weights the difference is considerably greater in both cases (Text-fig. 5). This provides additional evidence of the tendency of the Oxford cross for longer bones.

Table 23. *Significance of breed differences*

Lambs: 33–40 lb. carcass weight. Length of left fore-cannon.

–18.59 S. Standard error per sheep = 3.8% of mean.

Average mm.	Iceland	B.L. \times Iceland	Black- faced	B.L. \times Black- faced	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	122.6	N.S.	S.	S.	S.	N.S.	1.907	5
B.L. \times Iceland	N.S.	122.5	S.	S.	S.	N.S.	2.132	4
Black-faced	S.	S.	109.111	s.	N.S.	S.	1.421	9
B.L. \times Black-faced	S.	S.	s.	113.928	S.	s.	1.140	14
Southdown \times B.L.-Chev.	S.	S.	N.S.	S.	107.782	S.	0.8891	23
Oxford \times B.L.-Chev.	N.S.	N.S.	S.	s.	S.	119.5	2.132	4

S. = significant $P = 0.01$.s. = significant $P = 0.05$.

N.S. = not significant.

Table 24. *Significance of breed differences*

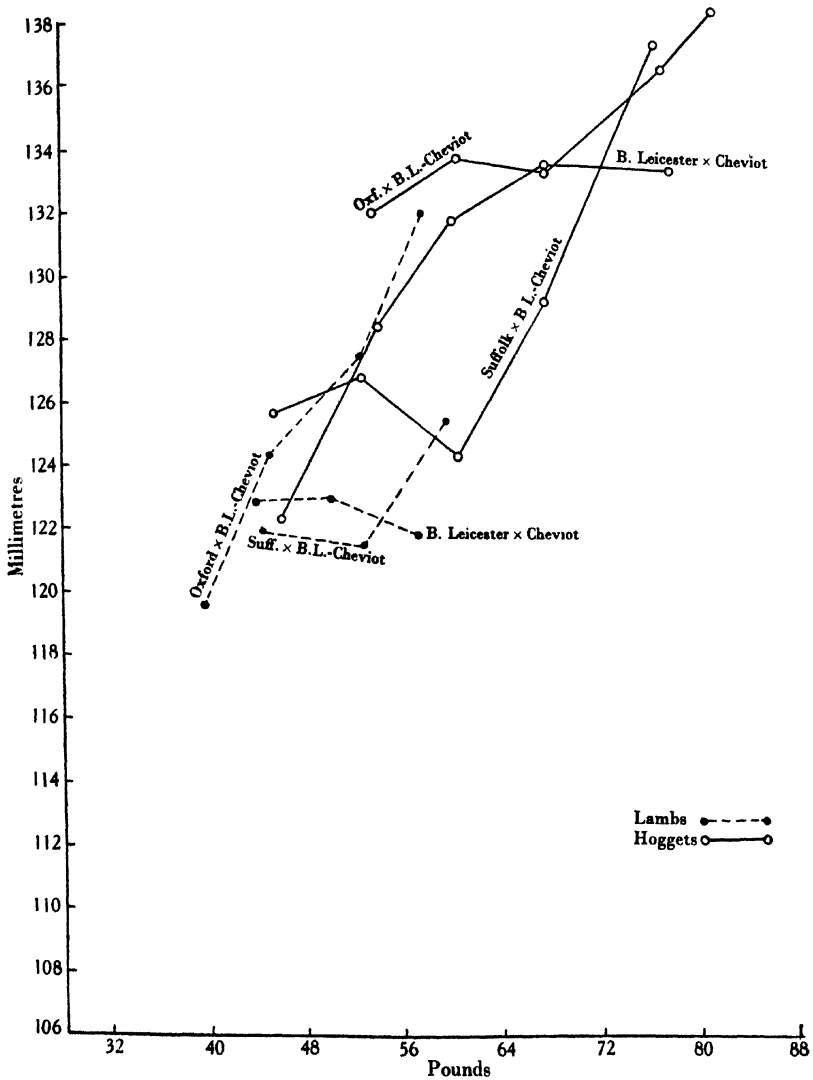
Lambs: 41–48 lb. carcass weight. Length of fore-cannon.

 $F = 10.23$ S. Standard error per sheep = 4.4% of mean.

Average mm.	Iceland	B.L. \times Iceland	B.L. \times Black- faced	B.L. \times Chev.	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	Suffolk \times B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	130.667	N.S.	S.	N.S.	S.	N.S.	s.	3.0725	3
B.L. \times Iceland	N.S.	126.80	S.	N.S.	S.	N.S.	N.S.	2.380	5
B.L. \times Black-faced	S.	S.	116.125	s.	N.S.	S.	s.	1.8815	8
B.L. \times Chev.	N.S.	N.S.	s.	122.75	S.	N.S.	N.S.	2.661	4
Southdown \times B.L.-Chev.	S.	S.	N.S.	S.	112.417	S.	S.	1.536	12
Oxford \times B.L.-Chev.	N.S.	N.S.	S.	N.S.	S.	124.15	N.S.	1.190	20
Suffolk \times B.L.-Chev.	s.	N.S.	s.	N.S.	S.	N.S.	121.875	1.8815	8

S. = significant $P = 0.01$ s. = significant $P = 0.05$.

N.S. = not significant.



Text-fig. 5. Changes with breed, age and weight. Length of cannon bone.

(b) *Minimum circumference.*

The significance of breed differences in the minimum circumference of the left fore-cannon is given in Tables 25 and 26. It is striking that the Blackfaced at the lower weight and the B.L. × Blackfaced at both weights have significantly slenderer bones than any other breed with the exception of the Iceland at 41–48 lb. The other breeds do not differ significantly from each other except the Southdown × B.L.-Cheviot at 33–40 lb., which has a slenderer cannon than the Oxford × B.L.-Cheviot and the B.L. × Iceland. Another feature of interest is the relatively great difference between the B.L. × Blackfaced and the B.L. × Cheviot, the latter having a much larger circumference. This difference can only be attributed to the influence of the mother breeds.

Table 25. *Significance of breed differences*

Lambs: 33–40 lb. carcass weight. Circumference of left fore-cannon.

 $F=6.29$ S. Standard error per sheep = 3.7% of mean.

Average mm.	Iceland	B.L. × Iceland	Black- faced	B.L. × Black- faced	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	45.6	N.S.	s.	s.	N.S.	N.S.	0.7501	5
B.L. × Iceland	N.S.	47.0	S.	S.	s	N.S.	0.8387	4
Blackfaced		S.	43.333	N.S.	s.	S.	0.5591	9
B.L. × Blackfaced		S.	N.S.	43.714	s.	S.	0.1483	14
Southdown × B.L.-Chev.		s.	s	s	45.0	S.	0.3498	23
Oxford × B.L.-Chev.		N.S.	S.	S.	S.	47.5	0.8387	4

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

Table 26. *Significance of breed differences*

Lambs: 41–48 lb. carcass weight. Circumference of fore-cannon.

 $F=3.54$ S. Standard error per sheep = 5% of mean.

Average mm.	Iceland	B.L. × Iceland	B.L. × Black- faced	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	46.607	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	1.371	3
B.L. × Iceland	N.S.	48.20	S.	N.S.	N.S.	N.S.	N.S.	1.062	5
B.L. × Blackfaced	N.S.	S.	44.50	S.	S.	S.	S.	0.8398	8
B.L. × Chev.	N.S.	N.S.	S.	49.25	N.S.	N.S.	N.S.	1.188	4
Southdown × B.L.-Chev.	N.S.	N.S.	S.	N.S.	47.583	N.S.	N.S.	0.6857	12
Oxford × B.L.-Chev.	N.S.	N.S.	S.	N.S.	N.S.	48.50	N.S.	0.5311	20
Suffolk × B.L.-Chev.	N.S.	N.S.	S.	N.S.	N.S.	N.S.	48.875	0.8398	8

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

(c) *Weight.*

The Blackfaced and Southdown × B.L.-Cheviot have significantly lighter cannons than the other breeds at 33–40 lb. (Table 27). That of the B.L. × Blackfaced is only slightly heavier at this weight, but at

41-48 lb. it is similar to the Southdown \times B.L.-Cheviot (Table 28). The Oxford \times B.L.-Cheviot has at both weights the heaviest bone but does not differ significantly from the B.L. \times Iceland at both weights, and the Iceland and Suffolk \times B.L.-Cheviot at 41-48 lb. The B.L. \times Cheviot has a heavier cannon than the B.L. \times Blackfaced. Though the Iceland has at both weights 8-10% lighter cannons than the B.L. \times Iceland, this difference is not quite significant at the 5% level, owing to the relatively high standard error per sheep.

Table 27. *Significance of breed differences*

Lambs: 33-40 lb. carcass weight. Weight of left fore-cannon.

$F = 14.92$ S. Standard error per sheep = 8.7% of mean.

Average mm.	Iceland	B.L. \times Iceland	Black- faced	B.L. \times Black- faced	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	41.40	N.S.	S.	s.	S.	s.	1.478	5
B.L. \times Iceland	N.S.	45.75	S.	S.	S.	N.S.	1.653	4
Blackfaced	S.	S.	35.444	N.S.	N.S.	S.	1.102	9
B.L. \times Blackfaced	s.	S.	N.S.	37.714	s.	S.	0.8837	14
Southdown \times B.L.-Chev.	S.	S.	N.S.	s.	35.434	S.	0.6894	23
Oxford \times B.L.-Chev.	s.	N.S.	S.	S.	S.	46.75	1.653	4

S. = significant $P = 0.01$.

s. = significant $P = 0.05$.

N.S. = not significant.

Table 28. *Significance of breed differences*

Lambs: 41-48 lb. carcass weight. Weight of fore-cannon.

$F = 7.64$ S. Standard error per sheep = 10.4% of mean.

Average g.	Iceland	B.L. \times Iceland	B.L. \times Black- faced	B.L. \times Chev.	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	Suffolk \times B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	45.333	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	2.810	3
B.L. \times Iceland	N.S.	49.0	S.	N.S.	S.	N.S.	N.S.	2.177	5
B.L. \times Blackfaced	N.S.	S.	40.375	s.	N.S.	S.	S.	1.721	8
B.L. \times Chev.	N.S.	N.S.	s.	48.25	s.	N.S.	N.S.	2.434	4
Southdown \times B.L.-Chev.	N.S.	S.	N.S.	s.	41.083	S.	S.	1.405	12
Oxford \times B.L.-Chev.	N.S.	N.S.	S.	N.S.	S.	50.35	N.S.	1.088	20
Suffolk \times B.L.-Chev.	N.S.	N.S.	S.	N.S.	S.	N.S.	49.875	1.721	8

S. = significant $P = 0.01$.

s. = significant $P = 0.05$.

N.S. = not significant.

The weight of left fore-cannon in lambs is very highly correlated with the weight of bone in the carcass (Part I, Table 1). An increase by 1 g. in weight of cannon means an increment of 46.6 g. in the weight of bone in the carcass. The average weight of total bone in the dressed carcass of Southdown \times B.L.-Cheviot and Oxford \times B.L.-Cheviot at 41-48 lb. calculated from the regression formula is 2249 g. in the former and 2682 g. in the latter. Therefore at 44 lb. a carcass of an Oxford \times B.L.-Cheviot contains practically 1 lb. or 19.2% more bone than a carcass of a Southdown \times B.L.-Cheviot.

(d) *Weight : length ratio (thickness of bone).*

The weight per unit length of the cannon is the best easily-measured indication of bone thickness. Tables 29 and 30 give the average weight in grams per cm. of the left fore-cannon bone length for the different breeds and the significance of these differences. At 33-40 lb. the Oxford × B.L.-Cheviot has the highest weight per unit length of cannon, closely followed by the B.L. × Iceland. These two differ significantly from all the other breeds which have practically the same weight : length ratio. At 41-48 lb. the Iceland and B.L. × Blackfaced have the lowest weight per unit length and the Suffolk × B.L.-Cheviot and Oxford × B.L.-Cheviot the highest. The B.L. × Cheviot and B.L. × Iceland show but slightly smaller figures and the Southdown cross is intermediate (Text-fig. 6).

Table 29. *Significance of breed differences*

Lambs: 33-40 lb. carcass weight. $\frac{\text{Weight}}{\text{Length}} \times 100$ of left fore-cannon.

$F=9.33$ S. Standard error per sheep = 8.3% of mean.

Average mm.	Iceland	B.L. × Iceland	Black- faced	B.L. × Black- faced	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	33.92	s.	N.S.	N.S.	N.S.	S.	0.9432	5
B.L. × Iceland	s.	37.325	S.	S.	S.	N.S.	1.0545	4
Blackfaced	N.S.	S.	32.522	N.S.	N.S.	S.	0.7030	9
B.L. × Blackfaced	N.S.	S.	N.S.	33.085	N.S.	S.	0.5637	14
Southdown × B.L.-Chev.	N.S.	S.	N.S.	N.S.	32.756	S.	0.4398	23
Oxford × B.L.-Chev.	S.	N.S.	S.	S.	S.	39.10	1.0545	4

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

Table 30. *Significance of breed differences*

Lambs: 41-48 lb. carcass weight. $\frac{\text{Weight}}{\text{Length}} \times 100$ of left fore-cannon.

$F=9.16$ S. Standard error per sheep = 6.4% of mean.

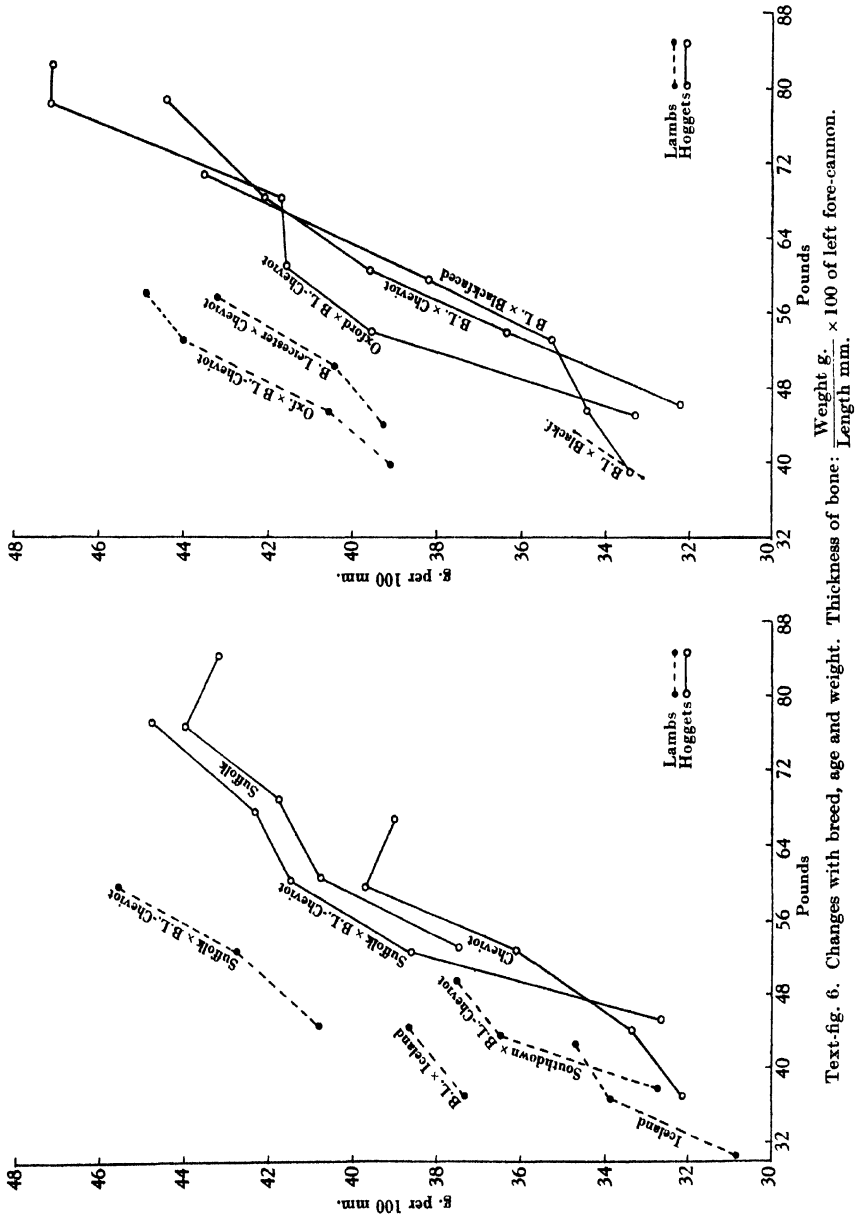
Average g. per 10 cm.	Iceland	B.L. × Iceland	Black- faced	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	34.70	s.	N.S.	s.	N.S.	S.	S.	1.425	3
B.L. × Iceland	s.	38.75	S.	N.S.	N.S.	N.S.	N.S.	1.104	5
B.L. × Blackfaced	N.S.	S.	34.75	S.	N.S.	S.	S.	0.8727	8
B.L. × Chev.	s.	N.S.	S.	39.275	N.S.	N.S.	N.S.	1.234	4
Southdown × B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	36.467	S.	S.	0.7126	12
Oxford × B.L.-Chev.	S.	N.S.	S.	N.S.	S.	40.555	N.S.	0.5519	20
Suffolk × B.L.-Chev.	S.	N.S.	S.	N.S.	S.	N.S.	40.80	0.8727	8

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

It is of interest to note that the difference between the weight : length ratio in the Southdown × B.L.-Cheviot as compared with the Oxford and Suffolk crosses with the B.L.-Cheviot is relatively greater than the differences in minimum circumference of cannon in these breeds. This is

Text-fig. 6. Changes with breed, age and weight. Thickness of bone: Weight g. $\times 100$ of left fore-cannon. Length mm.

due to the fact that there is a difference in the form of the cannon bones which cannot be expressed directly by length, weight or circumference measurements. In some breeds, i.e. Southdown \times B.L.-Cheviot, there is much less difference between the thickness of the middle of the shaft of the metacarpal and its extremities than in others, i.e. Oxford \times B.L.-Cheviot. In the former the extremities of the long bones are small relative to the shaft, while in the latter they are very thick and coarse, thus increasing the weight of the bones relatively more than does the minimum circumference of the shaft. This condition is illustrated in Pls. V and VI (see also Part III).

Nathusius (1880) found great differences in the relative length to breadth of the cannon bones of sheep. For the Southdown the length was 12 times the diameter, whereas in the Heath sheep it was 17 times. Hammond (1932) found in wethers of 5 months old that the early-maturing breeds have relatively thicker cannon bones (circumference) than late-maturing ones. In adult rams of different types he found that thickness growth was inhibited in the semi-wild breeds (Soay and Shetland) as compared with improved mutton breeds (Suffolk and Hampshire), while the wool type (Merino) was intermediate.

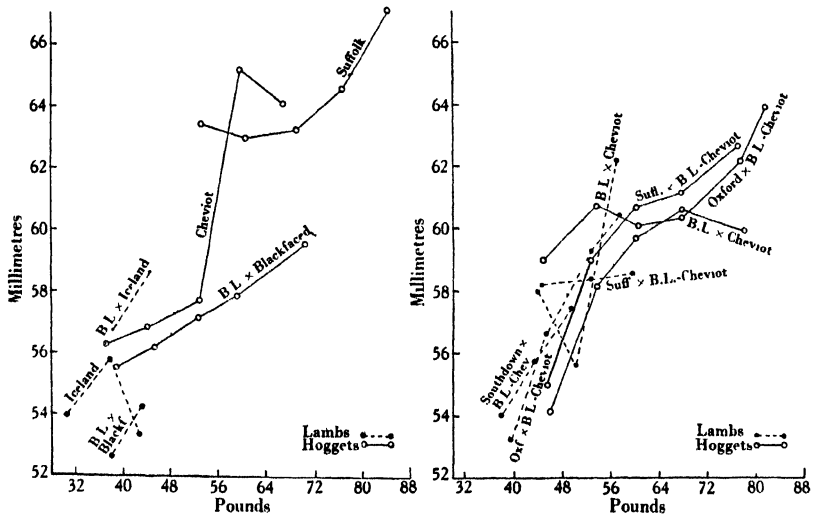
(3) "*Internal*" measurements

(a) *Measurements of muscle at the last rib.*

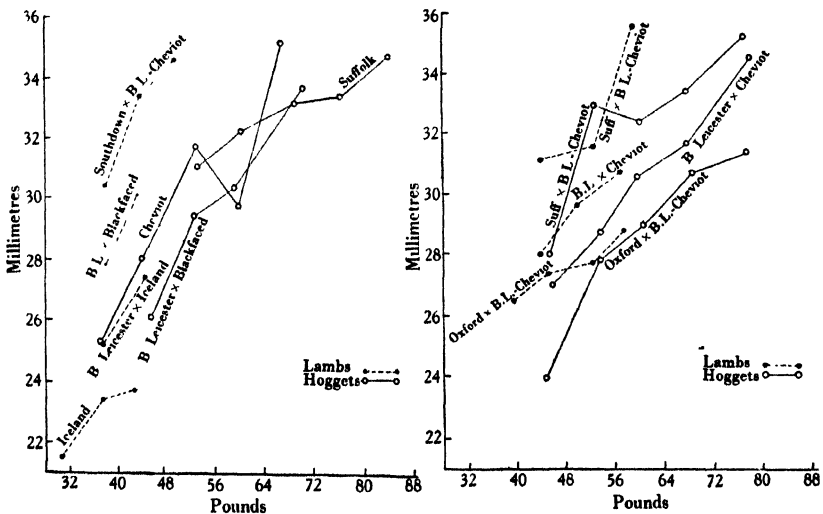
Length of eye muscle A. Tables 31 and 32 (Text-fig. 7) show that the various breeds do not differ greatly in length of eye muscle *A*. The difference between any two breeds is in no case significant at the 1 % level. The Blackfaced and B.L. \times Blackfaced have the shortest *A* at 33-40 lb., while the B.L. \times Iceland has the longest. At 41-48 lb. the Iceland has the smallest *A*, followed closely by B.L. \times Blackfaced, while the B.L. \times Iceland, Suffolk \times B.L.-Cheviot and B.L. \times Cheviot exceed the other breeds in this measurement.

Depth of eye muscle B. There are wide differences between the breeds in the depth of eye muscle *B* (Tables 33 and 34) (Text-fig. 8). The Southdown \times B.L.-Cheviot is significantly superior to all other breeds at both weights, with the exception of the Suffolk \times B.L.-Cheviot at 41-48 lb. The Blackfaced and B.L. \times Blackfaced follow the Southdown cross with a deep eye muscle at 33-40 lb. The Iceland, B.L.-Iceland and Oxford \times B.L.-Cheviot do not differ significantly between themselves at this weight, but are all significantly inferior to the other breeds.

At 41-48 lb. the B.L. \times Blackfaced has a deep eye muscle only slightly



Text-fig. 7. Changes with breed, age and weight. Length of eye-muscle (A).



Text-fig. 8. Changes with breed, age and weight. Depth of eye-muscle (B).

inferior to that of the Suffolk \times B.L.-Cheviot. The B.L. \times Cheviot is, on the other hand, slightly poorer than the B.L. \times Blackfaced. The Iceland has a very shallow eye muscle, significantly less than in all other breeds. The B.L. \times Iceland and Oxford \times B.L.-Cheviot have also very small B measurements.

Table 31. *Significance of breed differences*

Lambs: 33-40 lb. carcass weight. Length of eye muscle (A).

$F=2.81$ s. Standard error per sheep = 5.7% of mean.

Average mm.	Iceland	B.L. \times Iceland	Black- faced	B.L. \times Black- faced	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	55.8	N.S.	s.	N.S.	N.S.	N.S.	1.374	5
B.L. \times Iceland	N.S.	56.75	s.	s.	N.S.	N.S.	1.537	4
Blackfaced	s.	s.	51.222	N.S.	s.	N.S.	1.024	9
B.L. \times Blackfaced	N.S.	s.	N.S.	52.667	N.S.	N.S.	0.7936	15
Southdown \times B.L.-Chev.	N.S.	N.S.	s.	N.S.	54.044	N.S.	0.6409	23
Oxford \times B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	N.S.	53.25	1.537	4

S. = significant $P=0.01$. s. = significant $P=0.05$. N.S. = not significant.

Table 32. *Significance of breed differences*

Lambs: 41-48 lb. carcass weight. Length of eye muscle (A).

$F=2.34$ s. Standard error per sheep = 5.5% of mean.

Average mm.	Iceland	B.L. \times Iceland	B.L. \times Black- faced	B.L. \times Chev.	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	Suffolk \times B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	53.333	s.	N.S.	N.S.	N.S.	N.S.	s.	1.7945	3
B.L. \times Iceland	s.	58.6	s.	N.S.	N.S.	N.S.	N.S.	1.390	5
B.L. \times Blackfaced	N.S.	s.	54.25	N.S.	N.S.	N.S.	s.	1.099	8
B.L. \times Chev.	N.S.	N.S.	N.S.	58.0	N.S.	N.S.	N.S.	1.554	4
Southdown \times B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	55.75	N.S.	N.S.	0.8973	12
Oxford \times B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	N.S.	56.65	N.S.	0.6950	20
Suffolk \times B.L.-Chev.	s.	N.S.	s.	N.S.	N.S.	N.S.	58.222	1.036	9

S. = significant $P=0.01$. s. = significant $P=0.05$. N.S. = not significant.

Table 33. *Significance of breed differences*

Lambs: 33-40 lb. carcass weight. Depth of eye muscle (B).

$F=9.22$ S. Standard error per sheep = 8.7% of mean.

Average mm.	Iceland	B.L. \times Iceland	Black- faced	B.L. \times Black- faced	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	23.40	N.S.	S.	S.	S.	N.S.	1.099	5
B.L. \times Iceland	N.S.	25.25	N.S.	N.S.	S.	N.S.	1.229	4
Blackfaced	S.	N.S.	28.11	N.S.	s.	N.S.	0.8193	9
B.L. \times Blackfaced	S.	N.S.	N.S.	27.60	S.	N.S.	0.6346	15
Southdown \times B.L.-Chev.	S.	S.	s.	S.	30.43	S.	0.5125	23
Oxford \times B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	S.	26.50	1.229	4

S. = significant $P=0.01$. s. = significant $P=0.05$. N.S. = not significant.

Table 34. *Significance of breed differences*Lambs: 41-48 lb. carcass weight. Depth of eye muscle (*B*). $F=11.02$ S. Standard error per sheep = 8.3% of mean.

Average mm.	Iceland	B.L. × Iceland	B.L. × Black- faced	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	23.666	s.	S.	s.	S.	s.	S.	1.412	3
B.L. × Iceland	s.	27.40	N.S.	N.S.	S.	N.S.	S.	1.0935	5
B.L. × Blackfaced	S.	N.S.	30.125	N.S.	S.	s.	N.S.	0.8645	8
B.L. × Chev.	S.	N.S.	N.S.	28.0	S.	N.S.	s.	1.223	4
Southdown × B.L.-Chev.	s.	S.	S.	S.	33.333	S.	s.	0.7059	12
Oxford × B.L.-Chev.	s.	N.S.	S.	N.S.	S.	27.35	S.	0.5468	20
Suffolk × B.L.-Chev.	S.		N.S.				31.11	0.8151	

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

The shape index of eye muscle varies greatly with breed (Table 44*a*). The Southdown × B.L.-Cheviot has the best-shaped "eye", followed by the Blackfaced and B.L. × Blackfaced, while the Iceland, B.L. × Iceland and Oxford × B.L.-Cheviot have the lowest shape index.

The fact that the breeds differ much more in the depth than the length of "eye muscle" confirms Hammond's (1932) hypothesis that breeds differ much more in late than early developing characters. The latter are not so easily controlled by man, as they develop early in life and nutrition does not affect them nearly to the same extent as the late developing characters (McMeekan (1938) and later section of this paper). Breed improvement for meat consists therefore in acquiring greater development of these late-maturing, often very important characters. This can be best achieved by selection hand in hand with improved nutrition. Though increase in measurement *B* does not contribute more to the increase in the weight of muscle in the carcass than an increase in *A*, good development of the former is of much greater importance from the quality point of view (see Part I). A reduction in *A* with a corresponding increase in *B* is actually beneficial. As illustrated in Part I the shape index of eye muscle is negatively correlated with length of bone (cannon). Therefore long bone should be vigorously selected against, at least in those breeds intended for fat lamb production.

In the large, long-boned breeds, i.e. the Iceland, and Oxford × B.L.-Cheviot, more of the nutrients available to the lambs are utilized for bone growth than in small-boned breeds, i.e. Southdown × B.L.-Cheviot and Blackfaced. For the latter, therefore, more food is available for the development of such important economic qualities as thickness of muscle and fat. By very good nutrition in early life one can push forward the development of late-developing characters relative to that of earlier developing ones to a certain extent (see Part II, § III).

The strikingly small difference between the shape index in the Blackfaced and the Southdown \times B.L.-Cheviot lambs is contrary to what Hirzel (1936) found to be the case between the Blackfaced and the Southdown at 9 and 21 months. The Blackfaced had a shape index of 55 and the Southdown 61. This situation in our case may be explained by two causes. First, the Southdown \times B.L.-Cheviot may have a poorer shape index than the pure-bred Southdown owing to the influence of the mother breed. Secondly, the relatively great development of the depth of eye muscle in the Blackfaced lambs may be due to the very high plane of nutrition (relative to the normal for the breed) on which they must have been reared to reach this weight at the young age registered. This is suggestive of inherent capabilities of the Blackfaced to develop deep eye muscle. The explanation receives further confirmation from the B.L. \times Blackfaced cross which has a very good shape index, better than the B.L. \times Cheviot.

Thickness of muscle on the rib (X). The breed differences in this measurement can be seen in Appendix VI. We have not analysed the differences statistically, owing to possible errors involved in recording it. The breed differences are small, the Oxford \times B.L.-Cheviot, B.L. \times Iceland, and Iceland are the poorest, while the Southdown \times B.L.-Cheviot, the Blackfaced and Suffolk \times B.L.-Cheviot are slightly better. It will be noted that this order is in general agreement with that shown in respect to the eye muscle measures.

(b) *Measurements of fat at the last rib.*

C. With one major exception, the thickness of fat over the eye muscle varies but little in the different breeds (Tables 35 and 36). At 33-40 lb. the B.L. \times Blackfaced has significantly thicker back-fat than the other breeds with the exception of the B.L. \times Iceland. The latter does

Table 35. *Significance of breed differences*

Lambs: 33-40 lb. carcass weight. Depth of fat over eye muscle (C).

$P = 3.59$ S. Standard error per sheep = 37.9 % of mean.

Average mm.	Iceland	B.L. \times Iceland	Black- faced	B.L. \times Black- faced	South- down \times B.L.- Chev.	Oxford \times B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	2.60	N.S.	N.S.	S.	N.S.	N.S.	0.5760	5
B.L. \times Iceland	N.S.	3.25	N.S.	N.S.	N.S.	N.S.	0.6440	4
Blackfaced	N.S.	N.S.	2.667	S.	N.S.	N.S.	0.4293	9
B.L. \times Blackfaced	S.	N.S.	S.	4.533	S.	S.	0.3325	15
Southdown \times B.L.-Chev.	N.S.	N.S.	N.S.	S.	3.304	N.S.	0.2686	23
Oxford \times B.L.-Chev.	N.S.	N.S.	N.S.	S.	N.S.	2.50	0.6440	4

S. = significant $P = 0.01$.

s. = significant $P = 0.05$.

N.S. = not significant.

Table 36. *Significance of breed differences*

Lambs: 41-48 lb. carcass weight. Depth of fat over eye muscle (C).

 $F=3.76$ S. Standard error per sheep = 31.8% of mean.

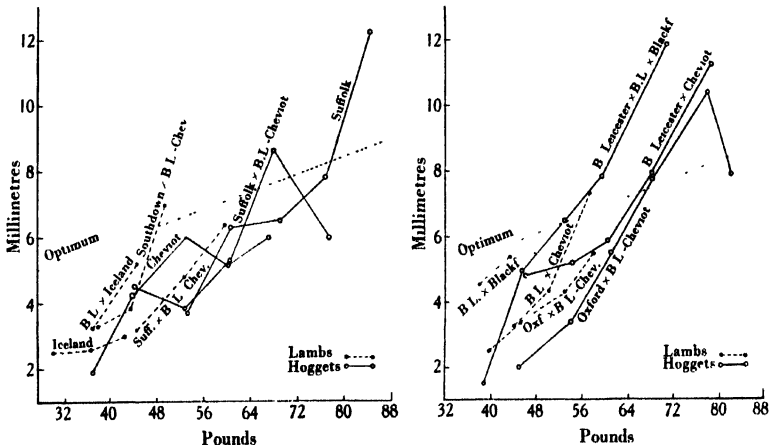
Average mm.	Iceland	B.L. × Iceland	B.L. × Black- faced	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	3.0	s.	s.	N.S.	N.S.	N.S.	N.S.	0.7606	3
B.L. × Iceland	s.	5.20	N.S.	s.	N.S.	s.	s.	0.5938	5
B.L. × Blackfaced	s.	N.S.	5.375	s.	s.	s.	s.	0.4694	8
B.L. × Chev.	N.S.	s.	s.	3.25	N.S.	N.S.	N.S.	0.6639	4
Southdown × B.L.-Chev.	N.S.	N.S.	s.	N.S.	3.833	N.S.	N.S.	0.3833	12
Oxford × B.L.-Chev.	N.S.	s.	s.	N.S.	N.S.	3.35	N.S.	0.2969	20
Suffolk × B.L.-Chev.	N.S.	s.	s.	N.S.	N.S.	N.S.	3.222	0.4126	9

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

not differ significantly, however, from the other breeds. The Oxford × B.L.-Cheviot is the leanest.

At 41-48 lb. the B.L. × Blackfaced and the B.L. × Iceland are practically alike in this measurement and differ significantly from all the breeds except that the latter does not differ significantly from the Southdown × B.L.-Cheviot. All the breeds, with the exception of B.L. × Blackfaced, and B.L. × Iceland at 41-48 lb., are rather too lean (Text-fig. 9),



Text-fig. 9. Changes with breed, age and weight. Thickness of fat over eye-muscle (C) in mm.

if one takes the Smithfield Show standards (calculated by Hirzel) as an ideal. Hirzel's standard is, however, based on animals at 9-21 months of age, and the same degree of fatness is not required in lambs.

J. At 33-40 lb. the B.L. × Blackfaced has a significantly larger *J* measurement (thickest fat on rib) than all the other breeds, with the exception of the Southdown × B.L.-Cheviot (Table 37). The latter has a significantly larger *J* than the Iceland and B.L. × Iceland.

Table 37. *Significance of breed differences*

Lambs: 33-40 lb. carcass weight. Thickest fat at last rib (J).

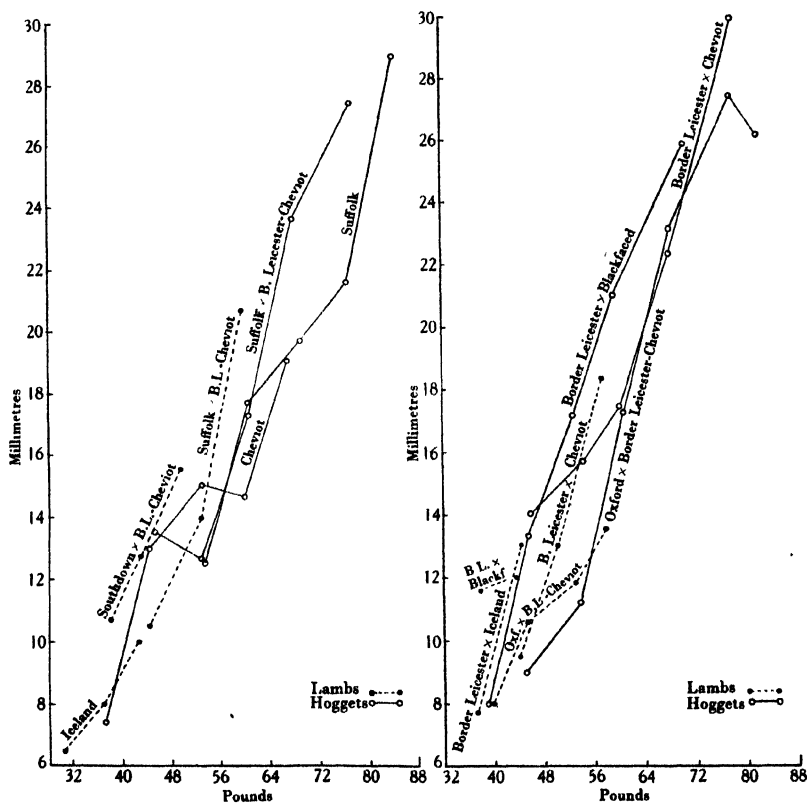
 $F = 3.43$ S. Standard error per sheep = 26.6 % of mean.

Average mm.	Iceland	B.L. × Iceland	Black- faced	B.L. × Black- faced	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	s.e. of mean	No. of individuals
Iceland	8.0	N.S.	N.S.	s.	s.	N.S.	1.191	5
B.L. × Iceland	N.S.	7.75	N.S.	s.	s.	N.S.	1.332	4
Blackfaced	N.S.	N.S.	8.666	s.	N.S.	N.S.	0.8880	9
B.L. × Blackfaced	s.	s.	s.	11.60	N.S.	s.	0.8878	15
Southdown × B.L.-Chev.	s.	s.	N.S.	N.S.	10.695	N.S.	0.5555	23
Oxford × B.L.-Chev.	N.S.	N.S.	N.S.	s.	N.S.	8.0	1.332	4

S. = significant $P = 0.01$.s. = significant $P = 0.05$.

N.S. = not significant.

At 41-48 lb. the breeds do not differ significantly in this measurement. The Southdown × B.L.-Cheviot, B.L. × Iceland and B.L. × Blackfaced are, however, slightly fatter at this point than the other breeds. None of the breeds can be said to be wastefully fat at these weights (Text-fig. 10).



Text-fig. 10. Changes with breed, age and weight. Thickest fat at last rib (J).

Y. The breed differences in measurement Y are very small at these weights (see Appendix VI). These have not been analysed statistically, owing both to the small differences between breeds and the possibility of inaccuracy in recording this measurement.

D. There are considerable breed differences in the depth of fat over the spinous process. However, due to very high standard error per sheep, only few of these are significant (Tables 38 and 39).

Table 38. *Significance of breed differences*

Lambs: 33–40 lb. carcass weight. Depth of fat over spine (D).

$F=6.00$ S. Standard error per sheep = 42.2% of mean.

Average mm.	Iceland	B.L. × Iceland	Black- faced	B.L. × Black- faced	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	1.20	N.S.	N.S.	S.	S.	N.S.	0.6835	5
B.L. × Iceland	N.S.	2.25	N.S.	N.S.	S.	N.S.	0.7641	4
Blackfaced	N.S.	N.S.	3.00	N.S.	S.	N.S.	0.5095	9
B.L. × Blackfaced	S.	N.S.	N.S.	3.733	N.S.	N.S.	0.3946	15
Southdown × B.L.-Chev.	S.	S.	S.	N.S.	4.695	s.	0.3187	23
Oxford × B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	s.	2.75	0.7641	4

S. = significant $P=0.01$.

s = significant $P=0.05$.

N.S. = not significant.

Table 39. *Significance of breed differences*

Lambs: 41–48 lb. carcass weight. Depth of fat over spine (D).

$F=3.15$ s. Standard error per sheep = 44.7% of mean.

Average mm.	Iceland	B.L. × Iceland	B.L. × Black- faced	B.L. × Chev.	South- down × B.L.- Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	S.E. of mean	No. of individuals
Iceland	2.00	N.S.	s.	N.S.	S.	N.S.	N.S.	1.0365	3
B.L. × Iceland	N.S.	4.20	N.S.	N.S.	N.S.	N.S.	N.S.	0.8029	5
B.L. × Blackfaced	s.	N.S.	4.50	N.S.	N.S.	N.S.	N.S.	0.6347	8
B.L. × Chev.	N.S.	N.S.	N.S.	2.50	S.	N.S.	N.S.	0.8976	4
Southdown × B.L.-Chev.	S.	N.S.	N.S.	S.	5.667	S.	S.	0.5182	12
Oxford × B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	S.	3.65	N.S.	0.4014	20
Suffolk × B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	S.	N.S.	3.444	0.5984	9

S. = significant $P=0.01$.

s = significant $P=0.05$.

N.S. = not significant.

The Southdown × B.L.-Cheviot at both weights exceeds the other breeds. The Iceland breed, on the other hand, has the thinnest layer of fat over the spine.

The small breed differences in back-fat, evident when comparisons are made at the same weight, are due to the control exercised by the farmer over the state of fatness of the carcass. Animals are not marketed unless they carry a reasonable cover of fat over the late developing loin region. Thus, the few individuals of a late developing breed which, due to individual variation in the direction of earlier maturity than characteristic for the breed in general and/or to a difference in the level of nutrition,

are marketed at a light weight, tend to carry as much fat as the earlier developing breeds frequent at this weight. If this degree of fatness is not present the animals are not marketed until higher weights. This tendency may be observed in Text-fig. 9. The earlier maturing breeds B.L. × Blackfaced and Southdown × B.L.-Cheviot are with few exceptions all marketed at lighter weights than the Oxford × B.L.-Cheviot and B.L. × Cheviot. It is only by experimental control of the material that a true measure of the degree of fatness at different ages and weights can be obtained. For the reason given above, differences amongst commercial carcasses tend to be masked.

The differences of 1–3 mm. in back-fat may appear very small and insignificant, but it must be borne in mind that at the critical points in the state of fatness of the animal a millimetre in either direction may make all the difference between first and second quality. If the animal is on the lean side 1 mm. fat cover all over the body can greatly improve the quality, while if it is too fat an extra millimetre increases greatly the wasteful fat.

The percentage differences in the fat measurement must be very high to be statistically significant owing to the large standard error per sheep. At 33–40 lb. the Southdown × B.L.-Cheviot has a 32 % larger *C* measurement than the Oxford × B.L.-Cheviot, but the difference is not significant.

B. CHANGES WITH WEIGHT IN CARCASS MEASUREMENTS

(1) *External measurements*

F and *T* (*leg length and length of tibia + tarsus*). The variations with increase in carcass weight in the leg length in different breeds are illustrated in Text-fig. 2. There is a general increase in leg length with weight increase in the lambs. This increase is, however, much more rapid in the Oxford × B.L.-Cheviot and the Iceland than in the other breeds. In the B.L. × Cheviot and its crosses with Southdown and Suffolk there is first an increase in *F*, followed by a decrease with rise in carcass weight. This shows the relatively low capacity of the Oxford cross and the Iceland to grow muscle relative to bone as compared with the other breeds.

The changes in *T* with an increase in carcass weight are illustrated in Text-fig. 3. From a comparison of Text-figs. 2, 3, which are to the same scale, it is clear that increase in *T* is more uniform than in *F*, which is to be expected, as muscle and fat development affect the latter, but not the former, which is an absolute bone measure. There is greater increase in *T*

with rise in body weight in the Oxford \times B.L.-Cheviot, Iceland and B.L. \times Iceland than in the other breeds. The slightly shorter T in the Suffolk \times B.L.-Cheviot and B.L. \times Cheviot at 57–64 than at 49–56 lb. may be due to small numbers represented.

The effect of weight on the difference between the leg length and the tibia-tarsus length ($F - T$) is given in Table 13. This difference decreases in all breeds with weight increase, with two minor exceptions. This shows that with an increase in body weight, though length of bones increases, the muscle increases relatively more so, filling the gap between the legs at a faster rate than it is increased by the length growth of the bones. Therefore (see Part I) the proportion of muscle to bone increases with weight in all the breeds.

G and H , width and depth of gigots. With an increase in carcass weight there is a regular increase both in G and H in all the breeds (Appendix VI). With an increase in carcass weight the compactness of the hindquarters increases, i.e. the width of the gigots G increases relatively more than the leg length F (Table 40). As illustrated in Part I, § I, this indicates an increase in the muscle : bone ratio with an increase in body weight. Table 40 shows that, in the Oxford \times B.L.-Cheviot and the Iceland, the compactness of the gigots increases very slowly with increase in carcass weight as compared with the other breeds. This further confirms the relatively undesirable conformation of these two breeds and their tendency to develop too much bone relative to muscle and fat.

Length of body, L . There is a considerable increase in L with increased carcass weight in all breeds (Table 41). The rate of increase in L mm. per 8 lb. increase in carcass weight varies from 17 mm. in the B.L. \times Cheviot and Oxford \times B.L.-Cheviot up to 28 mm. in the B.L. \times Iceland and the Iceland.

Table 40. *Shape of hindquarters ($G/F \times 100$) in lambs*

Breed	Weight classes, lb.				
	25–32	33–40	41–48	49–56	57–64
Iceland	77.2	83.0	80.3	—	—
B.L. \times Iceland	—	82.5	84.2	—	—
Blackfaced	—	91.4	—	—	—
B.L. \times Blackfaced	—	85.7	88.0	—	—
B.L. \times Chev.	—	—	87.1	88.4	94.0
Southdown \times B.L.-Chev.	—	94.0	97.3	100.6	—
Oxford \times B.L.-Chev.	—	82.4	84.7	85.6	85.4
Suffolk \times B.L.-Chev.	—	—	89.7	90.1	95.3

Depth of thorax (Th). The changes in the depth of thorax with increase in carcass weight are shown in Table 42. There is an increase in all the breeds, at the rate of about 7 mm. per 8 lb. increase in carcass weight,

Table 41. *Length of body (L) in mm. in lambs of different weights*

Breed	Weight classes, lb.				
	25-32	33-40	41-48	49-56	57-64
Iceland	555	578	612	—	—
B.L. × Iceland	—	602	630	—	—
Blackfaced	—	562	—	—	—
B.L. × Blackfaced	—	587	609	—	—
B.L. × Chev.	—	—	599	619	633
Southdown × B.L.-Chev.	—	555	577	598	—
Oxford × B.L.-Chev.	—	596	608	647	649
Suffolk × B.L.-Chev.	—	—	617	638	657

except in the Suffolk × B.L.-Cheviot which only increases by 1.5 mm. per 8 lb. The percentage increase is therefore practically the same in body length and depth of thorax, which indicates that ribs increase in length at approximately the same rate as the vertebral column with increase in body weight.

Table 42. *Depth of thorax (Th) in mm. in lambs at different weights*

Breed	Weight classes, lb.				
	25-32	33-40	41-48	49-56	57-64
Iceland	266	275	277	—	—
B.L. × Iceland	—	272	281	—	—
Blackfaced	—	249	—	—	—
B.L. × Blackfaced	—	257	264	—	—
B.L. × Chev.	—	—	260	270	275
Southdown × B.L.-Chev.	—	250	260	265	—
Oxford × B.L.-Chev.	—	262	275	280	284
Suffolk × B.L.-Chev.	—	—	276	278	279

(2) *Canon-bone measurements*

Length. Text-figs. 4 and 5 show the variation in the length of the left fore-cannon bone (metacarpal) in the lambs of different breeds with increase in carcass weight. There is a considerable increase in this measurement in all the breeds except the B.L. × Cheviot. From the slopes of the curves it is clear that the rate of increase is greater in the Iceland and the Oxford × B.L.-Cheviot than the other breeds. The Iceland and the B.L. × Iceland lambs actually have longer canons than both lambs and hoggets of any other breed at the same weight. This shows clearly the excessive legginess of the Iceland breed.

Weight and weight : length ratio. Table 43 shows the increase in weight of the left fore-cannon bone with increase in carcass weight for lambs. The rate of absolute weight increase in bone is nearly twice as high in the Oxford × B.L.-Cheviot, the Iceland and Suffolk × B.L.-Cheviot as in the B.L. × Cheviot and the B.L. × Blackfaced.

From Text-fig. 6 it is obvious that the rate of weight increase in the

cannon is much greater than the rate of length increase, i.e. the weight : length ratio of the cannon increases greatly with increase in carcass weight in all breeds. This illustrates that though bones grow simultaneously in length and thickness (weight per unit length) they grow at a faster rate in thickness in the later stages of development, i.e. length of bones is an earlier developing character than thickness (Hammond, 1932). The weight : length ratio increases with weight at a faster rate in Southdown \times B.L.-Cheviot over the range from 33 to 48 lb. than in any other breed, indicating the relatively earlier development of the Southdown cross. The decline in the slope of the curve for the weight class 49–56 lb. cannot be considered significant due to the small number of representatives.

Table 43. *The weight of left fore-cannon (g.) in lambs at different carcass weights*

Breed	Weight classes, lb.				
	25–32	33–40	41–48	49–56	57–64
Iceland	36.5	41.4	45.3	—	—
B.L. \times Iceland	—	45.8	49.0	—	—
Blackfaced	—	35.4	—	—	—
B.L. \times Blackfaced	—	37.7	40.1	—	—
B.L. \times Chev.	—	—	48.2	49.0	52.7
Southdown \times B.L.-Chev.	—	35.1	41.1	40.5	—
Oxford \times B.L.-Chev.	—	46.0	50.4	56.0	59.2
Suffolk \times B.L.-Chev.	—	—	49.9	51.8	57.0

(3) “Internal” measurements

(a) *Muscle measurements.*

The changes in length *A* and depth *B* of the eye muscle with increase in weight of the lambs of the different breeds are illustrated in Text-figs. 7, 8 (both to the same scale). Though there is an increase in both measurements with weight increase in all the breeds the relative rate at which *A* and *B* increase varies considerably with breed. The smaller *A* in the Iceland at 41–48 than at 33–40 lb. and in the B.L.-Cheviot at 49–56 than at 41–48 lb. can only be explained as an irregularity due to the small number of individuals represented in these weight classes.

The greatest breed differences in rate of development of *A* and *B* are met with in the Oxford \times B.L.-Cheviot and the Suffolk \times B.L.-Cheviot. In the former *A* increases at a much faster rate than *B*, while in the latter the position is reversed. The B.L. \times Cheviot is in an intermediate position as regards *B*, but approaches more the Oxford \times B.L.-Cheviot in respect of *A*. In the case of the Southdown \times B.L.-Cheviot both *A* and *B* increase greatly with weight, but the latter at a faster rate. This shows the

influence of the ram breed used on the B.L. × Cheviot ewe. The Oxford has a detrimental effect on quality while the Suffolk and still more the Southdown effect marked improvements. In the B.L. × Blackfaced both *A* and *B* increase greatly with weight and at practically the same rate.

Table 44

(a) *Shape index of "eye" muscle ($B/A \times 100$) in wether lambs of different breeds*

Breed	Weight classes, lb.				
	25-32	33-40	41-48	49-56	57-64
Iceland	39.80	41.90	46.37	—	—
Border Leicester	—	44.48	46.92	—	—
Blackfaced	—	55.23	—	—	—
B.L. × Blackfaced	—	52.98	55.80	—	—
B.L. × Chev.	—	—	48.30	53.25	49.20
Southdown × B.L.-Chev.	—	56.36	60.01	60.00	—
Oxford × B.L.-Chev.	—	49.78	48.43	46.68	47.52
Suffolk × B.L.-Chev.	—	—	53.75	53.95	60.41

(b) *Shape index of "eye" muscle ($B/A \times 100$) in wether hoggets of different breeds*

Breed	Weight classes, lb.						
	33-40	41-48	49-56	57-64	65-72	73-80	81-88
B.L. × Blackfaced	51.35	46.59	51.48	52.46	56.30	—	—
Cheviot	44.91	49.37	55.00	45.58	54.69	—	—
B.L. × Chev.	—	49.85	49.26	51.19	52.13	55.38	—
Oxford × B.L.-Chev.	—	40.68	45.72	48.16	50.70	50.20	57.00
Suffolk × B.L.-Chev.	—	50.90	55.69	53.21	54.37	55.77	—
Suffolk	—	—	48.92	51.26	50.76	51.49	51.49

The rate of increase in *B* relative to *A* is best illustrated in Table 44 by the changes in the shape index $\frac{B \times 100}{A}$. This increases with weight in all the breeds except in the Oxford × B.L.-Cheviot, where it actually decreases up to 49-56 lb. This indicates the unsuitability of the latter for lamb production as the early developing, less important characters grow at a faster rate than the late developing important characters even up to heavy weights. This must be attributed to the inherent capabilities of this breed to grow to a large size and heavy weight as well as its relatively late development.

(b) *Fat measurements at last rib.*

In all the breeds there is a rise in measurement *C* and *J* with increase in carcass weight (Text-figs. 9, 10). The increase in mm. per 8 lb. carcass weight is much smaller at *C* than at *J*, as can be seen from the slopes of the curves. The dotted line across Text-fig. 9 shows the optimum amount of fat at *C*, based on Hirzel's standards (1936). It will be noted

that only in two cases in the lambs does *C* exceed the optimum, i.e. in Southdown \times B.L.-Cheviot at 49–56 lb. and B.L.-Cheviot at 57–64 lb. At the lower weights all breeds but the B.L. \times Blackfaced are rather too lean at this point, even allowing for less fat requirements in lambs than are indicated by Hirzel's standards (calculated for 9–21 months old animals). As referred to previously it is advantageous from the quality point of view that the difference in rate of fat deposition at *C* and *J* should be small, because at *J* excess fat tends to accumulate. By comparison of the curves for each breed in Text-figs. 9, 10 one can see the breed differences in this respect. The B.L. \times Blackfaced actually accumulates less fat at *J* than *C* from 33 to 48 lb. and differs outstandingly from all the other breeds. On the other hand *J* increases 7 times as much as *C* (absolute terms) from 25 to 48 lb. in the Iceland breed. *J* increases at a much faster rate than *C* in the Suffolk \times B.L.-Cheviot and the B.L. \times Iceland also.

§ II. COMPARISON OF THE DIFFERENT BREEDS AS HOGGETS (10–13 MONTHS OLD)

A. BREED DIFFERENCES AT A CONSTANT WEIGHT

(1) *External measurements*

F and *T* (length of leg and tibia + tarsus).

Table 45 shows the significance of the breed differences in leg length at 57–64 lb. The Cheviot (shortest) and the B.L. \times Blackfaced have significantly shorter legs than the Oxford \times B.L.-Cheviot and the Suffolk (longest). The Cheviot is also significantly shorter in the leg than the B.L. \times Cheviot. The other breeds are intermediate between these but the differences insignificant in either direction.

There are much greater breed differences in the length of tibia + tarsus *T* (Table 46). The Suffolk has significantly longer tibias than any of the other breeds. The Oxford \times B.L.-Cheviot and B.L. \times Cheviot are alike and have significantly longer tibias than the B.L. \times Blackfaced, Suffolk \times B.L.-Cheviot and the Cheviot. The Cheviot has the shortest tibia. At lower weights the breed differences are greater, see Text-figs. 2 and 3. This is particularly so in the case of the relatively short boned breeds such as the Cheviot and the B.L. \times Blackfaced. These have at 41–48 and 49–56 lb. very much shorter legs and tibias than the Suffolk \times B.L.-Cheviot, the Oxford \times B.L.-Cheviot and Suffolk. These conditions can only be explained by the fact that the relatively long boned individuals

Table 45. *Significance of breed differences*Hoggets: 57-64 lb. carcass weight, Leg length (*P*). $F=2.81$ s. Standard error per sheep = 5.0% of mean.

Average mm.	B.L. × Black-faced	Cheviot	B.L. × Chev.	Oxford × B.L.-Chev.	Suffolk × B.L.-Chev.	Suffolk	S.E. of mean	No. of individuals
B.L. × Blackfaced	274.808	N.S.	N.S.	s.	N.S.	s.	2.768	26
Cheviot	N.S.	266.714	s.	s.	N.S.	s.	5.335	7
B.L. × Chev.	N.S.	s.	280.0	N.S.	N.S.	N.S.	1.699	69
Oxford × B.L.-Chev.	s.	s.	N.S.	283.85	N.S.	N.S.	3.158	20
Suffolk × B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	277.44	N.S.	2.823	25
Suffolk	s.	s.	N.S.	N.S.	N.S.	286.308	3.915	13

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

Table 46. *Significance of breed differences*Hoggets: 57-64 lb. carcass weight, Length of tibia and tarsus (*T*). $F=7.81$ S. Standard error per sheep = 3.5% of mean.

Average mm.	B.L. × Black-faced	Cheviot	B.L. × Chev.	Oxford × B.L.-Chev.	Suffolk × B.L.-Chev.	Suffolk	S.E. of mean	No. of individuals
B.L. × Blackfaced	219.46	N.S.	s.	s.	N.S.	s.	1.523	26
Cheviot	N.S.	214.0	s.	s.	N.S.	s.	2.934	7
B.L. × Chev.	s.	s.	224.116	N.S.	s.	s.	0.9345	69
Oxford × B.L.-Chev.	s.	s.	N.S.	225.80	s.	s.	1.736	20
Suffolk × B.L.-Chev.	N.S.	N.S.	s.	s.	219.72	s.	1.552	25
Suffolk	s.	s.	s.	s.	s.	231.538	2.153	13

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

of the Cheviot and B.L. × Blackfaced do not become fat enough for sale until at heavy weights. The B.L. × Cheviot shows greater bone growth than the B.L. × Blackfaced as was the case in lambs (see § I). The fact that the Suffolk × B.L.-Cheviot has absolutely shorter tibia + tarsus than either of the parent breeds is not in accord with the theory that characters of this nature behave as intermediates in inheritance. There are several possible explanations. The Suffolk in this comparison was bred and fed in Cambridgeshire and environmental differences may have an effect, though this is extremely unlikely on such early developing character as bone length. It is more probable that the strain of Suffolk sheep from which rams in south-east Scotland are obtained are actually shorter in the bone than the strain of Suffolks bred in Cambridgeshire. It is also possible that more of the B.L. × Cheviot breeding ewes in south-east Scotland are derived from the Border strain of Cheviots, while many of the B.L. × Cheviot hoggets studied may have been bred from the North Country Cheviot. The latter is known to be "higher on the leg" than the Border strain of Cheviots and consequently the B.L. × Cheviot hoggets used in this study may be leggier than if they were all derived from the Border Cheviot.

The difference between the length of leg and the length of tibia + tarsus is illustrated in Table 47. The breed differences are not very great. The Cheviot is the best, but particularly at low weights. The Suffolk is relatively good at heavy weights, while the Oxford × B.L.-Cheviot is the poorest until it reaches 72 lb. At the heaviest weights the differences are not very reliable owing to the numbers involved.

Table 47. *Difference between the leg length and the length of tibia + tarsus in hoggets (F - T) in mm.*

Breed	Weight classes, lb.						
	33-40	41-48	49-56	57-64	65-72	73-80	81-88
B.L. × Blackfaced	63.0	56.6	55.4	55.3	53.5	—	—
Cheviot	52.3	45.0	50.3	52.7	51.0	—	—
B.L. × Chev.	—	59.5	56.0	56.0	55.6	56.0	—
Oxford × B.L.-Chev.	—	63.0	61.4	58.1	58.2	50.0	51.5
Suffolk × B.L.-Chev.	—	62.5	60.0	57.7	57.6	63.3	—
Suffolk	—	—	62.0	54.8	53.9	55.1	50.5

G and H (width and depth of gigots).

The Suffolk and the Suffolk × B.L.-Cheviot have much wider gigots *G* than all the other breeds (Table 48). The Suffolk has significantly greater *G* than the Suffolk × B.L.-Cheviot at the 5% level. The latter falls approximately midway between the parent breeds.

Table 48. *Significance of breed differences*

Hoggets: 57-64 lb. carcass weight. Width of gigots (*G*).

$F=15.73$ S. Standard error per sheep = 3.4% of mean.

Average mm.	B.L. × Blackfaced	Cheviot	B.L. × Chev.	Oxford × Chev.	Suffolk × Chev.	Suffolk	S.E. of mean	No. of individuals
B.L. × Blackfaced	251.42	N.S.	N.S.	N.S.	S.	S.	1.707	26
Cheviot	N.S.	248.67	N.S.	N.S.	S.	S.	3.290	7
B.L. × Chev.	N.S.	N.S.	253.46	N.S.	S.	S.	1.048	69
Oxford × B.L.-Chev.	N.S.	N.S.	N.S.	252.75	S.	S.	1.946	20
Suffolk × B.L.-Chev.	S.	S.	S.	S.	263.6	s	1.741	25
Suffolk	S.	S.	S.	S.	s.	270.8	2.414	13

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

Table 49. *Significance of breed differences*

Hoggets: 57-64 lb. carcass weight. Depth of gigots (*H*).

$F=4.78$ S. Standard error per sheep = 1.9% of mean.

Average mm.	B.L. × Blackfaced	Cheviot	B.L. × Chev.	Oxford × Chev.	Suffolk × Chev.	Suffolk	S.E. of mean	No. of individuals
B.L. × Blackfaced	141.346	N.S.	S.	S.	S.	N.S.	1.393	26
Cheviot	N.S.	140.0	s.	s.	s.	N.S.	2.685	7
B.L. × Chev.	S.	s.	146.19	N.S.	N.S.	S.	0.8553	69
Oxford × B.L.-Chev.	S.	s.	N.S.	148.05	N.S.	S.	1.5885	20
Suffolk × B.L.-Chev.	S.	S.	N.S.	N.S.	147.24	S.	1.421	25
Suffolk	N.S.	N.S.	S.	S.	S.	140.38	1.971	13

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

The Oxford \times B.L.-Cheviot, the Suffolk \times B.L.-Cheviot and the B.L. \times Cheviot have significantly larger *H* than the Suffolk, Cheviot and B.L. \times Blackfaced (see Table 49).

The shape of the hindquarters ($G/F \times 100$).

The breed differences in the shape index of the hindquarters are illustrated in Table 50. At 57–64 lb. the Oxford \times B.L.-Cheviot is the poorest. The Suffolk \times B.L.-Cheviot is the best in this respect, followed by the Suffolk and the Cheviot. At other weights the order of merit is slightly different. At the lower weights the Cheviot is of outstanding merit and good at all weights. The Suffolk and Suffolk \times B.L.-Cheviot closely approach it particularly at the heavier weights. The Oxford \times B.L.-Cheviot is inferior to all the breeds up to 72 lb.

Table 50. *Shape of hindquarters ($G/F \times 100$) in hoggets*

Breed	Weight classes, lb.						
	33–40	41–48	49–56	57–64	65–72	73–80	81–88
B.L. \times Blackfaced	78.9	88.5	90.8	91.5	93.0	—	—
Cheviot	92.9	95.2	93.2	93.2	97.4	—	—
B.L. \times Chev.	—	89.8	91.2	90.5	93.6	97.4	—
Oxford \times B.L.-Chev.	—	77.1	87.3	89.0	91.9	97.8	96.1
Suffolk \times B.L.-Chev.	—	84.1	92.0	95.0	95.9	92.5	—
Suffolk	—	—	91.5	94.6	96.2	95.7	97.9

Length of body L.

At 57–64 lb. the Cheviot has a significantly shorter body than all the other breeds with the exception of B.L. \times Blackfaced (Table 51). The latter is shorter than the B.L. \times Cheviot, the Suffolk and Oxford \times B.L.-Cheviot. The Oxford \times B.L.-Cheviot has the longest body.

Table 51. *Significance of breed differences*

Hoggets: 57–64 lb. carcass weight. Length of body (L).

$F=4.20$ S. Standard error per sheep = 2.9 % of mean.

Average mm.	B.L. \times Black- faced	Oxford \times Suffolk \times				Suffolk	S.E. of mean	No. of individuals
		Cheviot	B.L. \times Chev.	B.L. \times Chev.	B.L. \times Chev.			
B.L. \times Blackfaced	635.96	N.S.	s.	S.	N.S.	s.	3.658	26
Cheviot	N.S.	622.857	S.	S.	s.	S.	7.0495	7
B.L. \times Chev.	s.	S.	645.36	N.S.	N.S.	N.S.	2.245	69
Oxford \times B.L.-Chev.	S.	S.	N.S.	653.0	s.	N.S.	4.1705	20
Suffolk \times B.L.-Chev.	N.S.	s.	N.S.	s.	639.2	N.S.	3.730	25
Suffolk	s.	S.	N.S.	N.S.	N.S.	648.846	5.173	13

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

At other weights the breeds fall in the same order of increasing body length, but they differ more in the lower weight classes (see Table 62). The benefit of the extra body length of the Oxford \times B.L.-Cheviot is

largely nullified by the fact that it is associated with a relatively thinner "eye muscle" in this breed (Text-figs. 7, 8).

(2) Cannon-bone measurements

Length of cannon.

The breed differences in length of the left fore-cannon at 57–64 lb. are shown in Table 52. The breeds fall in two groups. The Suffolk × B.L.-Cheviot, Cheviot and B.L. × Blackfaced have significantly shorter cannons than the other breeds. These latter do not differ significantly though the Oxford cross has slightly longer cannons than the others. Text-fig. 5 shows that the Suffolk × B.L.-Cheviot has slightly shorter cannons at 57–64 lb. than at the lower weight classes. This can only be due to the small number represented at 41–48 and 49–56 lb. At lower weights the Cheviot has much shorter cannons than the B.L. × Blackfaced. As in the case of the lambs the B.L. × Cheviot has longer bones than the B.L. × Blackfaced. The Southdown × B.L.-Cheviot at 41–48 lb. has the shortest cannons of all the breeds, though those of the Cheviot (represented in greater numbers) are but slightly longer.

Table 52. *Significance of breed differences*

Hoggets: 57–64 lb. carcass weight. Length of left fore-cannon.

$F = 12.79$ S. Standard error per sheep = 3.8 % of mean.

Average mm.	B.L. × Black- faced	Cheviot	B.L. × Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	Suffolk	S.E. of mean	No. of individuals
B.L. × Blackfaced	125.0	N.S.	S.	S.	N.S.	s.	1.180	18
Cheviot	N.S.	124.833	S.	S.	N.S.	N.S.	2.045	6
B.L. × Chev.	S.	S.	131.545	N.S.	S.	N.S.	0.6165	66
Oxford × B.L.-Chev.	S.	S.	N.S.	133.5	S.	N.S.	1.120	20
Suffolk × B.L.-Chev.	N.S.	N.S.	S.	S.	124.167	S.	1.180	18
Suffolk	s	N.S.	N.S.	N.S.	S.	130.0	1.771	8

s. = significant $P = 0.01$.

s. = significant $P = 0.05$.

N.S. = not significant.

Circumference of cannon.

The Oxford × B.L.-Cheviot has a significantly greater minimum circumference of the left fore-cannon than the other breeds (Table 53). The Suffolk has the smallest minimum circumference and differs significantly from the B.L. × Cheviot and the Suffolk × B.L.-Cheviot.

Weight of cannon.

Table 54 shows the significance of the breed differences. The B.L. × Blackfaced has the lightest cannon, but does not differ significantly from the Cheviot. The Oxford × B.L.-Cheviot has significantly heavier bones than all the other breeds with the exception of the Suffolk.

Table 53. *Significance of breed differences*

Hoggets: 57-64 lb. carcass weight. Circumference of left fore-cannon.

 $F=5.55$ S. Standard error per sheep = 4.8% of mean.

Average mm.	B.L. × Black- faced		Oxford × B.L.- Chev.		Suffolk × B.L.- Chev.		S.E. of mean	No. of individuals
	Cheviot	Chev.	Chev.	Chev.	Suffolk	Suffolk		
B.L. × Blackfaced	50.889	N.S.	N.S.	S.	N.S.	N.S.	0.5940	18
Cheviot	N.S.	51.333	N.S.	s.	N.S.	N.S.	1.029	6
B.L. × Chev.	N.S.	N.S.	52.016	S.	N.S.	S.	0.3102	66
Oxford × B.L.-Chev.	S.	s.	S.	54.10	s.	S.	0.5635	20
Suffolk × B.L.-Chev.	N.S.	N.S.	N.S.	s.	52.389	S.	0.5940	18
Suffolk	N.S.	N.S.	S.	S.	S.	49.25	0.8910	8

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

Table 54. *Significance of breed differences*

Hoggets: 57-64 lb. carcass weight. Weight of left fore-cannon.

 $F=5.87$ S. Standard error per sheep = 8.9% of mean.

Average g.	B.L. × Black- faced		Oxford × B.L.- Chev.		Suffolk × B.L.- Chev.		S.E. of mean	No. of individuals
	Cheviot	Chev.	Chev.	Chev.	Suffolk	Suffolk		
B.L. × Blackfaced	47.8	N.S.	S.	S.	s.	s.	1.0655	18
Cheviot	N.S.	49.567	N.S.	S.	N.S.	N.S.	1.897	6
B.L. × Chev.	S.	N.S.	52.147	S.	N.S.	N.S.	0.5765	65
Oxford × B.L.-Chev.	S.	S.	S.	55.665	S.	N.S.	1.039	20
Suffolk × B.L.-Chev.	s.	N.S.	N.S.	S.	51.517	N.S.	1.0955	18
Suffolk	s.	N.S.	N.S.	N.S.	N.S.	52.95	1.643	8

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

Weight : length ratio of cannon (thickness of bone).

The Oxford × B.L.-Cheviot and the Suffolk × B.L.-Cheviot have significantly greater weight per unit length of bone than the B.L. × Blackfaced and the B.L. × Cheviot at 57-64 lb. (Table 55). The other breeds do not differ significantly. The B.L. × Blackfaced has the lowest weight : length ratio. The difference between the Oxford × B.L.-Cheviot and the other breeds is still greater at 49-56 and 73-80 lb. At 33-40 and 41-48 lb. the B.L. × Blackfaced slightly exceeds the Cheviot in this measurement (see Text-fig. 6).

Table 55. *Significance of breed differences*Hoggets: 57-64 lb. carcass weight. $\frac{\text{Weight}}{\text{Length}} \times 100$ of left fore-cannon. $F=3.39$ S. Standard error per sheep = 7.8% of mean.

Average g. per 10 cm.	B.L. × Black- faced		Oxford × B.L.- Chev.		Suffolk × B.L.- Chev.		S.E. of mean	No. of individuals
	Cheviot	Chev.	Chev.	Chev.	Suffolk	Suffolk		
B.L. × Blackfaced	38.228	N.S.	N.S.	S.	N.S.	N.S.	0.7316	18
Cheviot	N.S.	39.683	N.S.	N.S.	N.S.	N.S.	1.267	6
B.L. × Chev.	N.S.	N.S.	39.594	s.	s.	S.	0.3850	65
Oxford × B.L.-Chev.	S.	N.S.	s.	41.625	N.S.	N.S.	0.6940	20
Suffolk × B.L.-Chev.	S.	N.S.	N.S.	N.S.	41.461	N.S.	0.7316	18
Suffolk	N.S.	N.S.	N.S.	N.S.	N.S.	40.738	1.097	8

S. = significant $P=0.01$.s. = significant $P=0.05$.

N.S. = not significant.

The effect of breed on the shape of the left fore-cannon at constant weight for different weight classes is illustrated in Pls. VII-X. The slenderness of the B.L. × Blackfaced cannons is marked, particularly at the lower weights. The Oxford × B.L.-Cheviot has on the other hand extremely coarse bones at all weights. The extremities of the latter are much thicker than in any of the other breeds. As this greatly increases the weights of the bones it should be selected against.

(3) "Internal" measurements

(a) Muscle measurements at the last rib.

Length of "eye" A. The general trend of the breed differences is illustrated in Text-fig. 7. The significance of these differences at 57-64 lb. is given in Table 56. The B.L. × Blackfaced has the shortest "eye" muscle. The Suffolk and the Cheviot have significantly longer *A* measurements than the other breeds. At lower weights the difference between the Cheviot and the B.L. × Blackfaced is much smaller and appears to be insignificant.

Table 56. *Significance of breed differences*

Hoggets: 57-64 lb. carcass weight. Length of eye muscle (*A*).

$F=8.73$ S. Standard error per sheep = 5.2% of mean.

Average mm.	B.L. × Blackfaced	Cheviot	B.L. × Cheviot	Oxford × B.L.-Cheviot	Suffolk × B.L.-Cheviot	S.E. of mean	No. of individuals
B.L. × Blackfaced	57.85	S.	S.	S.	S.	0.6165	26
Cheviot	S.	65.143	S.	S.	N.S.	1.188	7
B.L. × Cheviot	S.	S.	59.754	N.S.	S.	0.3784	69
Oxford × B.L.-Cheviot	S.	S.	N.S.	60.15	N.S.	0.7029	20
Suffolk × B.L.-Cheviot	S.	S.	N.S.	N.S.	60.72	0.6287	25
Suffolk	S.	N.S.	S.	S.	62.923	0.8718	13

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

Table 57. *Significance of breed differences*

Hoggets: 57-64 lb. carcass weight. Depth of eye muscle (*B*).

$F=5.86$ S. Standard error per sheep = 7.8% of mean.

Average mm.	B.L. × Blackfaced	Cheviot	B.L. × Cheviot	Oxford × B.L.-Cheviot	Suffolk × B.L.-Cheviot	S.E. of mean	No. of individuals
B.L. × Blackfaced	30.308	N.S.	N.S.	N.S.	S.	0.4696	26
Cheviot	N.S.	29.714	N.S.	N.S.	S.	0.9049	7
B.L. × Cheviot	N.S.	N.S.	30.493	S.	S.	0.2883	69
Oxford × B.L.-Cheviot	N.S.	N.S.	S.	28.90	S.	0.5353	20
Suffolk × B.L.-Cheviot	S.	S.	S.	S.	32.280	0.4788	25
Suffolk	S.	S.	S.	S.	32.154	0.6640	13

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

Depth of "eye" muscle B. The Oxford × B.L.-Cheviot has the shallowest "eye" muscle but does not differ significantly from the Cheviot

and B.L. × Blackfaced. The Suffolk and Suffolk × B.L.-Cheviot have significantly deeper "eye" muscle than the other breeds (Table 57). The Cheviot at 57–64 lb. has a relatively smaller *B* than at other weights (Text-fig. 8). This irregularity in the curve must be due to the relatively small number represented.

The shape index $B/A \times 100$. The significance of the breed differences in the shape index of "eye" muscle is given in Table 58. The Cheviot and the Oxford × B.L.-Cheviot have the lowest shape index, while the Suffolk × B.L.-Cheviot and the B.L. × Blackfaced have the highest. At other weights the Cheviot has relatively better shape index, but otherwise the breed differences are much the same (Table 44*b*).

Table 58. *Significance of breed differences*

Hoggets: 57–64 lb. carcass weight. Shape index of "eye muscle" $B/A \times 100$.

$F=5.57$ S. Standard error per sheep = 8.9 % of mean.

Average mm.	B.L. × Black- faced	Cheviot	B.L. × Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	Suffolk	S.E. of mean	No. of individuals
B.L. × Blackfaced	52.46	S.	N.S.	S.	N.S.	N.S.	0.9080	26
Cheviot	S.	45.58	S.	N.S.	S.	S.	1.750	7
B.L. × Chev.	N.S.	S.	51.19	S.	N.S.	N.S.	0.5574	69
Oxford × B.L.-Chev.	S.	N.S.	s.	48.16	S.	N.S.	1.035	20
Suffolk × B.L.-Chev.	N.S.	S.	N.S.	S.	53.21	N.S.	0.9260	25
Suffolk	N.S.	S.	N.S.	N.S.	N.S.	51.26	1.284	13

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

(*b*) *Measurements of fat at the last rib.*

C. Table 59 shows that B.L. × Blackfaced has most fat at *C*. The other breeds do not differ significantly, but the Suffolk comes closest to the B.L. × Blackfaced in state of fatness. At other weights the trend of breed differences is much the same except that the Oxford × B.L.-Cheviot is relatively much leaner at the lower weights.

J. The B.L. × Blackfaced has also significantly greater *J* measurement than any of the other breeds. The Cheviot is the leanest. However,

Table 59. *Significance of breed differences*

Hoggets: 57–64 lb. carcass weight. Depth of fat over eye muscle (*C*).

$F=4.63$ S. Standard error per sheep = 36.5 % of mean.

Average mm.	B.L. × Black- faced	Cheviot	B.L. × Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	Suffolk	S.E. of mean	No. of individuals
B.L. × Blackfaced	7.846	S.	S.	S.	S.	S.	0.4342	26
Cheviot	S.	5.143	N.S.	N.S.	N.S.	N.S.	0.8368	7
B.L. × Chev.	S.	N.S.	5.898	N.S.	N.S.	N.S.	0.2666	69
Oxford × B.L.-Chev.	S.	N.S.	N.S.	5.50	N.S.	N.S.	0.4951	20
Suffolk × B.L.-Chev.	S.	N.S.	N.S.	N.S.	5.240	N.S.	0.4428	25
Suffolk	s.	N.S.	N.S.	N.S.	N.S.	6.307	0.6140	13

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

due to the high standard error per sheep, this difference of 18% is not significant at the 5% level. The other breeds are practically identical in this measurement (Table 60).

Table 60. *Significance of breed differences*

Hoggets: 57-64 lb. carcass weight. Thickest fat at last rib (*J*).

$F=3.92$ S. Standard error per sheep = 23.8% of mean.

Average mm.	B.L. × Black- faced	Cheviot	B.L. × Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	Suffolk	S.E. of mean	No. of individuals
B.L. × Blackfaced	20.923	S.	S.	S.	S.	s.	0.8325	26
Cheviot	S.	14.571	N.S.	N.S.	N.S.	N.S.	1.604	7
B.L. × Chev.	S.	N.S.	17.391	N.S.	N.S.	N.S.	0.5110	69
Oxford × B.L.-Chev.	S.	N.S.	N.S.	17.25	N.S.	N.S.	0.9492	20
Suffolk × B.L.-Chev.	S.	N.S.	N.S.	N.S.	17.20	N.S.	0.8490	25
Suffolk	s.	N.S.	N.S.	N.S.	N.S.	17.615	1.177	13

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

Table 61. *Significance of breed differences*

Hoggets: 57-64 lb. carcass weight. Depth of fat over spine (*I*).

$F=4.00$ S. Standard error per sheep = 38.5% of mean.

Average mm.	B.L. × Black- faced	Cheviot	B.L. × Chev.	Oxford × B.L.- Chev.	Suffolk × B.L.- Chev.	Suffolk	S.E. of mean	No. of individuals
B.L. × Blackfaced	7.385	N.S.	N.S.	N.S.	N.S.	s.	0.5360	26
Cheviot	N.S.	5.428	N.S.	N.S.	N.S.	S.	1.033	7
B.L. × Chev.	N.S.	N.S.	7.101	N.S.	N.S.	S.	0.3290	69
Oxford × B.L.-Chev.	N.S.	N.S.	N.S.	5.800	N.S.	S.	0.6111	20
Suffolk × B.L.-Chev.	N.S.	N.S.	N.S.	N.S.	6.880	S.	0.5466	25
Suffolk	s.	S.	S.	S.	S.	9.769	0.7580	13

S. = significant $P=0.01$.

s. = significant $P=0.05$.

N.S. = not significant.

D. Table 61 shows that the Suffolk has significantly thickest fat over the spinous process. The other breeds do not differ significantly.

B. CHANGES WITH WEIGHT IN CARCASS MEASUREMENTS

(1) *External measurements*

F and *T*. Text-fig. 2 illustrates the changes in leg length *F* with increase in carcass weight in the different breeds. The same general trend is apparent in all the breeds. At low weights the leg length is relatively great. With an increase in body weight it becomes shorter and with further weight increase the leg length increases greatly, in most cases ultimately reaching greater length than at the low weights. In the small breeds, particularly the Cheviot, *F* increases at much greater rate than in the large breeds, i.e. Suffolk and Oxford × B.L.-Cheviot.

Text-fig. 3 illustrates the general trend of changes in the length of tibia + tarsus with increased carcass weight. There is a small but steady

increase in tibia length with increased weight, with two exceptions at low weights, which are most likely due to small numbers. (Oxford \times B.L.-Cheviot at 41-48 and B.L. \times Blackfaced at 33-40 lb.)

The rate of increase is much greater in the smaller breeds (Cheviot and B.L. \times Blackfaced) than in the large breeds. This is probably due to the fact that the long boned individuals of the small breeds have to be carried to much higher body weight than the others to become of marketable quality. The relatively greater leg length at the low weights can best be explained by the fact that due to age the animals have already attained much of their length growth in bones. The low carcass weight on the other hand causes the latter to lack muscular development, which may be due to poor nutrition.

Table 47 shows the changes in the difference between *F* and *T* with increase in body weight. At low weights this difference is great in all breeds, but it decreases with an increase in weight, further illustrating that at the same age an increase in body weight results in relatively better proportions of muscle to bone.

G and H. The width and depth of the gigots increases in all breeds with increased carcass weight (see Appendix VI). The breeds differ very little in the rate of the increase.

The changes in the shape index of the hindquarters ($G/F \times 100$) with increase in body weight are given in Table 50. There is an increase in this ratio with body weight in all breeds. The rate of increase is less in the Cheviot and the Suffolk than in other breeds. It is highest in the Oxford \times B.L.-Cheviot, followed by the B.L. \times Blackfaced, which are, particularly the former, very poor at light weights.

L. Length of body increases in all breeds with increased carcass weight (see Table 62). The rate of increase varies with breed. The large breeds Suffolk and Oxford \times B.L.-Cheviot only increase by 40-50 mm. per 40 lb. carcass weight increase, while the Cheviot and the B.L. \times Blackfaced increase in length by twice the amount with corresponding weight increase. By comparison of Table 62 and Text-fig. 3 it is obvious that

Table 62. *Body length (L) in mm. in hoggets*

Breed	Weight classes, lb.					
	33-40	41-48	49-56	57-64	65-72	73-80 81-88
B.L. \times Blackfaced	570	596	615	636	679	— —
Cheviot	557	572	605	623	650	— —
B.L. \times Chev.	—	609	622	645	660	660 —
Oxford \times B.L.-Chev.	—	640	646	653	665	673 685
Suffolk \times B.L.-Chev.	—	607	605	639	649	676 —
Suffolk	—	—	626	649	658	671 679

the body length and the length of the tibia+tarsus increase at comparable rates and follow the same trend. The short legged breeds have the shortest bodies, so these two variates appear to be positively correlated.

(2) *Cannon-bone measurements*

Length of cannon. Text-figs. 4, 5 and Pls. XI and XII show the changes in the length of the left fore-cannon with increased body weight. The trend is the same as in the tibia+tarsus length. In the small breeds, the Cheviot and B.L. × Blackfaced, the cannon length increases at much greater rate than in the large breeds, i.e. the Suffolk and the Oxford × B.L.-Cheviot. The very long cannons in the Cheviot at 65–72 lb. can be due to small numbers.

Weight and weight : length ratio of cannon. Table 63 shows the increase in the weight of the left fore-cannon bone with increase in carcass weight in the different breeds. With 40 lb. increase in body weight the cannon bones increase from 40 to 50 % in weight in all the breeds but the Suffolk, where this increase is about 20 %. The much greater increase in weight than length of the cannon with an increase in body weight is clearly illustrated in Text-fig. 6. The slopes of the curves for the different breeds show that the trend of increase in the weight : length ratio is much the same in all the breeds. At low weights the rise is not so rapid in the Cheviot and the B.L. × Cheviot as the others. Over the 40 lb. range the weight per unit length of cannon increases from 17 to 41 %, being least in the Suffolk but greatest in the Oxford × B.L.-Cheviot.

Table 63. *Weight of left fore-cannons in hoggets (g.)*

Breed	Weight classes, lb.						
	33-40	41-48	49-56	57-64	65-72	73-80	81-88
B.L. × Blackfaced	39.9	41.3	43.6	47.8	50.5	—	—
Cheviot	36.4	37.7	43.3	49.6	54.0	—	—
B.L. × Chev.	—	39.4	46.7	52.2	56.1	59.1	—
Oxford × B.L.-Chev.	—	46.3	52.4	55.7	55.6	64.35	64.8
Suffolk × B.L.-Chev.	—	41.0	48.9	51.5	54.6	61.33	—
Suffolk	—	—	47.6	53.0	51.0	57.8	55.5

Since the weight differences within a breed are mainly due to difference in the level of nutrition, either external or internal, this shows how a low plane of nutrition affects thickness growth of bones more than the length growth. Pls. XI and XII show the effect of weight on the thickness and shape of the left fore-cannon in the Suffolk and the B.L. × Blackfaced. The greater slimness of the bones at light weights is marked, but more so in the smaller breed. Our results agree with those of Chirvinsky (1909), who found that in sheep with insufficient nourish-

ment the bones retained those peculiarities of shape which are typical of youth and were more slender than in well fed animals of the same breed.

(3) "*Internal*" measurements

(a) *Muscle measurements at the last rib.*

Text-figs. 7, 8 show the changes in length and depth of eye-muscle with increase in body weight in the different breeds. Both measurements increase with weight and *B* at a faster rate than *A*. The breeds do not vary much in the rate of increase in *A* and *B* with weight, except that at light weights *A* increases very slowly while *B* increases rapidly (see slope of curves in Text-figs. 7, 8).

The rate of increase in *B* relative to *A* is best illustrated in Table 44*b* by the changes in the shape index $B/A \times 100$. In all the breeds the shape index increases with weight. In the Suffolk this increase is only 5% with an increase in carcass weight from 49 to 56 to 81–88 lb., but it exceeds 20% in the Oxford \times B.L.-Cheviot. The latter, however, has throughout the poorest shape index except at 81–88 lb., and in that weight class only few individuals occur.

(b) *Fat measurements at the last rib.*

C and J. Text-figs. 9, 10 illustrate the changes in state of fatness with weight in the different breeds. There is an increase in fat, both at *C* and *J*, with increase in body weight in all the breeds. The rate of increase in fat with weight is much greater than in either muscle or bone.

The increase in measurement *C* with a 70–100% increase in carcass weight varies from about 130% in the Suffolk \times B.L.-Cheviot up to 700% in the B.L. \times Blackfaced. The corresponding increase in *J* varies from 110% in the former to 225% in the latter. In all the breeds, however, the absolute increase in mm. at *J* is approximately twice as great as at *C* (see Text-figs. 9, 10). At low weights there is greater deficiency in *C* than *J*, which indicates that the former is more severely affected by low plane of nutrition.

The optimum line across Text-fig. 9 shows at what weight hoggets of the different breeds reach the ideal state of fatness. The B.L. \times Blackfaced has attained this state at 49–56 lb. and is not very deficient at 41–48 lb. At 65–72 lb. this cross is excessively fat. The other breeds with the exception of the Cheviot are not fat enough to be classed as first quality until at 65–72 lb. However, they lack but little in this respect at 57–64 lb. The B.L. \times Cheviot and Oxford \times B.L.-Cheviot are too fat at

73–80 lb. but the Suffolk is not over-fat until above 80 lb. The Oxford × B.L.-Cheviot and Suffolk × B.L.-Cheviot are far too lean under 56 lb. The Cheviot is inclined to be slightly too lean at all the weights at which it is represented, but seriously so at 33–40 lb. At *J* all the breeds except Suffolk and Cheviot are rather too fat when they reach 65–72 lb.

§ III. CHANGES WITH AGE IN CARCASS MEASUREMENTS

A. EXTERNAL MEASUREMENTS

F and T. Text-fig. 2 illustrates the changes in leg length *F* due to increase in age from lambs (4–5 months) to hoggets (10–13 months) in the four breeds which are represented at both ages. In all the breeds except in the Oxford × B.L.-Cheviot at 57–64 lb. *F* is greater in the hoggets of the same breed and weight. This is most marked in the Suffolk × B.L.-Cheviot and the B.L. × Blackfaced. The length of the tibia + tarsus is also less in the lambs than in the hoggets at the same weight. The trend of the changes in the tibia and leg length is much the same (Text-figs. 2, 3). With an increase in age at constant carcass weight, length of bone increases.

G and H. There is a slight increase in width and depth of the gigots with age increase at constant weight (Appendix VI). The shape of the hindquarters ($G/F \times 100$) is practically alike in lambs and hoggets of the same breed at constant weight (Tables 40 and 50). However, at the lowest weights at which both lambs and hoggets are present the lambs have more compact hindquarters. The width of the hindquarters which are affected by the bony structure (pelvis) as well as muscle development is relatively more affected by very poor nutrition than is the leg length.

L. There is only a slight difference in body length between lambs and hoggets of the same breed and weight (Tables 41 and 62).

B. CANNON-BONE MEASUREMENTS

Length. The length of the cannon is slightly shorter in the lambs than the hoggets at constant weight. The greatest difference (5%) is met with in the B.L. × Blackfaced at 33–40 lb., while in the Oxford × B.L.-Cheviot at 57–64 lb. this difference is practically nil.

Minimum circumference. Table 64 shows the changes in minimum circumference of the cannon with increase in age from lambs to hoggets at constant weight. The lambs have more slender cannons than the hoggets in the B.L. × Blackfaced. In the other breeds at 41–48 lb. the

lambs have greater minimum circumference of cannon. At 49-56 lb. both lambs and hoggets are practically alike, while at 57-64 lb. the hoggets have greater minimum circumference than the lambs. This gives a good picture of the relatively early development of the B.L. × Black-faced as compared with the other breeds. The thickness growth of the shaft of the cannon, which is a late developing character, has been able to develop to a relatively greater extent in the B.L. × Blackfaced hoggets than in the other breeds. The poor nutrition of the hoggets has affected the B.L. × Blackfaced much less than the other breeds. In hoggets at 41-48 lb. the cannon of this breed has an absolutely greater minimum circumference than have the other breeds, though at the same age at higher weights (Appendix VI, and Table 53), when nutrition has not interfered with the innate growth tendencies to the same extent, it has an absolutely thinner bone as compared with the other breeds. The latter, as later maturing breeds, show a proportionately greater response to high nutrition.

Table 64. *Minimum circumference of left fore-cannon in lambs and hoggets at the same weight*

Weight classes, lb.	Age	B.L. × Blackfaced	B.L. × Chev.	Oxford × B.L.-Chev.	Suffolk × B.L.-Chev.
33-40	Lambs	43.7	—	—	—
	Hoggets	46.5	—	—	—
41-48	Lambs	44.5	49.2	48.5	48.9
	Hoggets	46.1	46.5	46.0	45.5
49-56	Lambs	—	48.9	50.7	50.2
	Hoggets	—	49.9	51.0	50.4
57-64	Lambs	—	50.3	51.5	50.8
	Hoggets	—	52.0	54.1	52.4

Weight. In Tables 43 and 63 the weight of the left fore-cannon in lambs and hoggets of the same weight is given. The cannons in the B.L. × Blackfaced lambs are lighter than those of the hoggets at the same weight. These weight differences are however very small as compared with the difference in length and minimum circumference. The lambs of the B.L. × Cheviot and its crosses with the Suffolk and Oxford have considerably heavier cannon bones than the hoggets at the same weight. This is striking at 49-56 lb., where the lambs of these breeds have cannons absolutely shorter and thinner than the hoggets but 5-7% heavier. This shows that poor nutrition may affect the weight of the bones beyond what can be measured by either length or circumference. This is further illustrated by the comparison of Text-fig. 6 and Table 64. The weight : length ratio of the cannon is higher in lambs than hoggets at the same weight. In all the breeds at all weights in which lambs and

hoggets occur, except in B.L. \times Blackfaced at 33–40 lb., the lambs show a considerably larger weight : length ratio. The absolutely shorter but heavier cannon bones in the lambs at the same weight as the hoggets show how a late developing character (bone thickness) can be pushed forward in development relatively to an early developing one (bone length) by high level of nutrition in early life as compared with low level of nutrition for a much longer period.

C. "INTERNAL" MEASUREMENTS

(1) *Muscle measurements at last rib*

Text-figs. 7, 8 show the changes in length and depth of eye muscle with increase in age from 4–5 to 10–13 months. *A*, the length of eye muscle, is smaller in the lambs of the B.L. \times Blackfaced and the Oxford \times B.L.-Cheviot than in the hoggets of the same breeds at similar weights. In the Suffolk \times B.L.-Cheviot and B.L. \times Cheviot the lambs have greater *A* measurement at 41–48 lb. than the hoggets at the same weight. In the former the hoggets exceed the lambs in *A* measurements at heavier weights. In all the breeds depth of eye muscle in the lambs is greater than in the hoggets at the same weights with the exception of Suffolk \times B.L.-Cheviot at 49–56 lb. Table 44*a, b* illustrates the changes in shape index of the eye muscle with increase in age. In all the breeds except B.L. \times Cheviot at 41–48 and 57–64 lb. and Suffolk \times B.L.-Cheviot at 49–56 lb. the shape index is higher in the lambs than the hoggets at the same weight. This is another example of the effect of good nutrition permitting the animal to attain absolutely greater development of late developing characters.

(2) *Fat measurements at the last rib*

Text-figs. 9, 10 show the development of fat at *C* and *J* in lambs and hoggets of the same breeds and weight. The lambs of B.L. \times Blackfaced and the Oxford \times B.L.-Cheviot are fatter than the hoggets. The B.L. \times Cheviot and Suffolk \times B.L.-Cheviot lambs are leaner than the hoggets at 41–48 lb. and in the case of the former also at 49–56 lb. This shows the relatively great difficulty of getting lambs of these latter breeds fat enough at under 50 lb. carcass weight. It will be noticed that the difference in state of fatness of the lambs and hoggets at constant weight is but small, and less than the difference in thickness of bones. It is highly probable that the hoggets have been poorly fed except for a short period prior to killing. Owing to their relatively advanced age they have

passed their optimum time for rapid growth of bones and even of muscle, though these tissues have not ceased growing; so fat, which is the latest developing tissue of the body and which can accumulate at a fast rate even in adult life, is deposited at a relatively rapid rate during this short period of good nutrition. On the other hand if the change from bad to good nutrition had been gradual over a long period it is likely that the bone and muscle would have made up some of this deficiency, judging by McMeekan's (1938) results of keeping pigs on different levels of nutrition. He found that pigs kept on a low plane of nutrition over a long period had absolutely heavier bones and muscle at the same weight as others kept on high level of nutrition and killed at a younger age, even when the former were very much retarded in development of all their tissues for the first 4 months of postnatal life. The greater proportional response of fat to the change from low to high nutrition in the latter animals gives weight to our explanation of the fat differences between lambs and hoggets, while the absolutely lighter bones in the same animals are similarly in line with the relative bone differences between lambs and hoggets.

DISCUSSION

In this investigation it has been our major aim to provide a factual basis for the qualities of different breeds and crosses in respect of their suitability for meat production. Such evidence is essential if farmers, in their ever increasing need for greater efficiency of production, are to be able to measure successfully the merits of the material with which they work. This work should be regarded as a move in the direction of making available to the farmer a tabulated comparative record of the meat qualities of his sheep. This record is necessarily incomplete and in many respects inadequate, but nevertheless provides conclusive evidence of the nature and extent of many breed differences of economic importance. The study is subject to the usual difficulties necessarily associated with the analysis of data from material not under direct experimental control, and similarly shows "gaps" in numbers characteristic of such data. We are aware of the fact that these leave the work open to criticism. For this reason care has been taken throughout in interpretation, and in the weight given to the results obtained. It will be observed that in cases where the evidence has been considered conclusive, the statistical relationship considered receives strong support from the general trend of breed differences over wide weight ranges. While the study of larger numbers of individuals may eliminate many of our inconclusive results

it is considered that the major trends in breed differences, as observed by us, would not be altered.

From the evidence given in § I it is clear that some of the breeds and crosses under investigation are much better suited for the production of prime quality lamb than others. Lambs of some of the breeds are not marketed under 40 lb. This is an indirect measure of their unsuitability for the production of light weight lambs. For early lambs of light weight (from 33 to 48 lb.) the B.L. cross with the Blackfaced gives excellent results. The B.L.-Cheviot produces coarser framed and later maturing lambs than the B.L. × Blackfaced. Lambs of the former do not yield good quality carcasses under 48 lb. and realization of this fact by the farmer is probably the reason for their absence from the Edinburgh market during this investigation at weights under 40 lb. With the available data we are not in a position to arrive at any definite conclusions as to the cause of the difference in the meat qualities of these two crosses. The most likely explanation, however, is that the Blackfaced is either an earlier developing breed than the Cheviot or that ewes of the former are better milkers. Possibly both factors are concerned.

The differences in the crossbred lambs from the B.L. × Cheviot ewes and rams of the Southdown, Suffolk and Oxford breeds are of great practical importance. The Southdown ram can be strongly recommended for the production of early lambs of relatively light weight (30–50 lb.) from B.L. × Cheviot ewes. Southdown × B.L.-Cheviot lambs are of excellent quality and superior to either the Suffolk or Oxford crosses in all the most important characters at light weights. The Suffolk cross yields carcasses of very satisfactory quality at heavier weights. Rams of this breed can therefore be recommended where heavy lambs are, for economic reasons, the objective. The Oxford cross carcasses are of poor quality at all weights. There seems to be no apparent justification for using the Oxford ram if natural conditions permit the Southdown or Suffolk rams to be successfully employed.

The Iceland lambs yield carcasses of poor conformation, the breed showing up as a relatively unimproved type. This is emphasized by the relative quality of the B.L. × Iceland where the cross with the improved breed has resulted in better carcass quality. Due to the large size of the Iceland breed even more satisfactory results are likely to be obtained by crossing it with a smaller framed early maturing breed such as the Southdown. For light weight lamb production it appears to be more satisfactory to use a small early maturing ram breed in crossing than a large, though relatively early maturing breed (like the Suffolk), since at light

weights the latter are absolutely more immature. For the same reason it is likely that lambs of better carcass quality and earlier maturity could be produced by crossing Down rams with the B.L. × Blackfaced ewe than with the B.L. × Cheviot, as the latter is a larger framed and later developing breed. Research into the relative merits of the B.L. × Cheviot and B.L. × Blackfaced as ewe breeds for fat lamb production is very desirable.

The results from the Leeds experiments of crossing Cheviot and Masham ewes, the former with Ryeland, Shropshire, Southdown and Suffolk rams, and the latter with Leicester, Oxford and Suffolk rams, are interesting. The Suffolk × Cheviot lambs are of poorer grading quality than the other Cheviot crosses at the same weight, while of the Masham crosses the Suffolk cross lambs were the best. This agrees with our observations on the relative merits of the Southdown, Suffolk and Oxford as ram breeds.

The breed differences in hoggets are less marked than in lambs (§ II), as has already been discussed. This is presumably due to the relatively poor nutrition of the hoggets in early life (see description of the material), which exerts a differential effect upon the differentially developing tissues. As will be shown in Part III the breed differences in proportional development of the different tissues are greatest in the latest developing regions of the body (loin, pelvis). Both considerations emphasize the necessity for good feeding and environmental conditions for breed differences to express themselves. Our results, therefore, further confirm Hammond's (1932) hypothesis that under limited conditions of nutrition breed differences are not able to express themselves. He found that at birth breed differences in singles were much more marked than in twins and triplets.

Despite this limitation the B.L. × Blackfaced is however superior as compared with the other breeds, yielding carcasses of excellent quality from 40 to 64 lb. At heavier weights this cross becomes rather too fat. This, however, need not be considered a fault in the breed, for small joints are in high demand and the overfatness is avoided by slaughter at lighter weights. The Cheviot yields carcasses of good conformation and quality at light to medium weights—40–60 lb. However, it is inclined to be too lean on the back and to develop excessive fat round the kidneys and in the neck (see Part III). Hammond (1921) found that the internal fat—caul and mesenteric—was greater in the Mountain breeds than in the Longwool and Down breeds. As in lambs the Oxford × B.L.-Cheviot yields hoggets of poorer mutton quality than the other breeds, particu-

larly at light weights. It has heavy, long bones, poor muscular development, and is far too lean at light weights. All the larger breeds however yield carcasses of satisfactory quality from 57 to 72 lb.

In hogget production where the price per lb. is less than in lambs, and where in consequence the price margin per lb. between good and medium quality carcasses is also less, weight is of considerable importance. Thus the small early maturing breeds such as the Southdown are likely to be less suitable for hoggetting than large breeds, even if these latter yield carcasses of lower quality. The extra weight obtainable without over-fattening from the large breeds may more than compensate for the lower price per lb. characteristic of heavy carcasses and/or inferior quality. Moreover the earlier maturing breeds may be less capable of thriving under the relatively severe environmental conditions normally associated with hogget production.

SUMMARY

Data on carcass quality measurements and weights of lambs and hoggets of various Scottish breeds and crosses have been analysed statistically. In addition, data on lambs of the Iceland breed and its cross with the Border Leicester as well as hoggets of the Suffolk breed have been incorporated in this study.

1. At constant carcass weight marked breed differences in body conformation exist. The Southdown \times B.L.-Cheviot has the most desirable conformation, while the Iceland and Oxford \times B.L.-Cheviot have the poorest.

2. The weight of bone in the carcass varies greatly with breed, as judged by the weight of the left fore-cannon. The small and/or early maturing breeds, viz. Southdown \times B.L.-Cheviot, Blackfaced and B.L. \times Blackfaced have much lighter skeletons than the larger and/or later maturing ones, viz. Oxford \times B.L.-Cheviot, Suffolk \times B.L.-Cheviot, B.L. \times Cheviot and B.L. \times Iceland.

3. Great breed differences in the degree of development of the muscles at the last rib are met with. The short boned breeds Southdown \times B.L.-Cheviot, B.L. \times Blackfaced and Blackfaced appear more early developing in this respect than the long boned breeds like the Oxford \times B.L.-Cheviot, Iceland and B.L. \times Iceland.

4. None of the breeds is too fat on the loin as lambs, but at light weights some, particularly the large framed types, are too lean. The B.L. \times Blackfaced appears to be the earliest developing cross in this respect.

5. All the breeds improve in carcass quality with an increase in weight within the limits of our data, but some relatively less than others. The Oxford \times B.L.-Cheviot improves less than the Suffolk \times B.L.-Cheviot with weight increase.

6. For the breeds and crosses studied there are less marked breed differences in the hoggets than in the lambs.

7. The B.L. \times Blackfaced yields the best quality hogget mutton of all the breeds, as shown by light bones, good muscular development and an optimum amount of fat. The Oxford \times B.L.-Cheviot yields carcasses of relatively inferior quality, having poor conformation, long and heavy bones, relatively poor muscular development and too little fat at low weights. The B.L. \times Cheviot is coarser boned and later maturing than the B.L. \times Blackfaced.

8. Up to a point the carcass quality in hoggets improves greatly with weight increase. Bones increase more in weight than in length, the eye muscle increases more in depth than in length and fat increases rapidly with increase in carcass weight. Only the smaller breeds, B.L. \times Blackfaced and Cheviot, yield carcasses of good quality from 40 to 56 lb. The other breeds are too lean at these weights. At over 72 lb. all the breeds become too fat except the Suffolk which is moderately fat till over 80 lb.

9. Lambs have better carcass quality than hoggets at the same weight. The latter have longer but relatively lighter bones, i.e. lower weight per unit length. The hoggets show less well-developed depth of eye muscle though length of eye muscle is in some cases greater. The shape index of eye muscle reaches a higher value in the lambs. There is little difference in the state of fatness on the loin.

10. The relative merits of the different breeds and crosses for lamb and mutton production are discussed in relation to practice. The importance of the ram breed as a factor affecting the quality of lambs from the B.L. \times Cheviot ewe is specially considered.

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LEFT FORE CANNON BONE EFFECT OF BREEDING
LAMBS OF WEIGHT CLASS 12-20 LBS

ICELAND

BORDER LEICESTER X ICELAND



BLACKFACED



BORDER LEICESTER X BLACKFACED



LUTHERAN X BORDER LEICESTER X CHEVIOT



OXFORD X BORDER LEICESTER X CHEVIOT



LEFT FORE CANNON BONE | EFFECT OF BREED
LAMBS. WEIGHT CLASS 47-49 LBS

ICELAND

BORDER LEICESTER X ICELAND



BORDER LEICESTER X BLACKFACED



BORDER LEICESTER X CHEVIOT



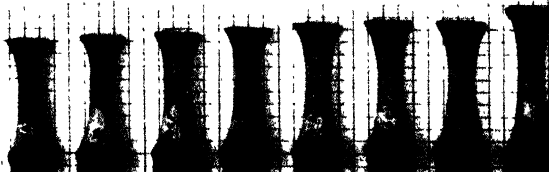
SOUTHDOWN X BORDER LEICESTER X CHEVIOT



OXFORD X BORDER LEICESTER X CHEVIOT



SUFFOLK X BORDER LEICESTER X CHEVIOT

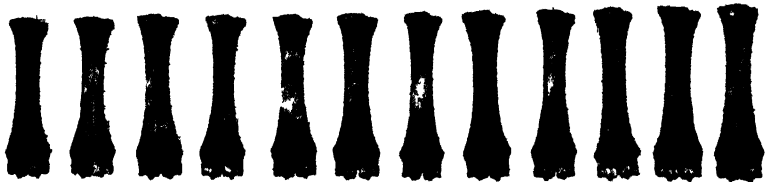


LEFT FORE CANNON BONE

EXPERIMENTAL BREED

HOGGET'S 2nd WEIGHT CLASS 41-48 LB.

MEASUREMENT



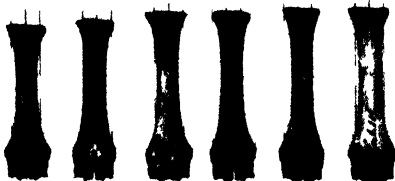
ROPER 1st CLASS 12-14 LB.



BUTTER 1st CLASS 12-14 LB.



COITDOWN 1st CLASS 12-14 LB.



LEFT FORE CANNON BONE
EFFECT OF BREED
HOGGETS OF WEIGHT CLASS 57-64 LBS

HORDEY LEICESTER X BLACKFACED



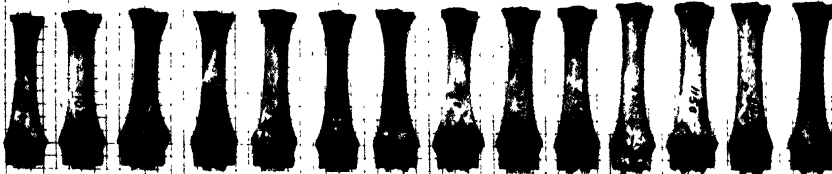
BOPDER LEICESTER X CHEVIOT



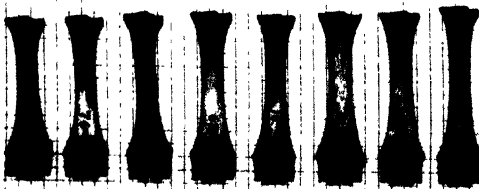
YORDEY LEICESTER X CHEV



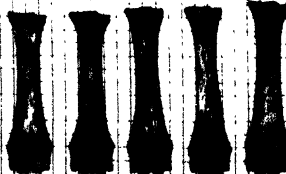
SUFFOLK X HORDEY LEICESTER X CHEVIOT



SUFFOLK



CHEVIOT



LEFT FORE CANNON BONE
EFFECT OF BREED
HOGGETS & WEIGHT CLASS 65-72 LB.

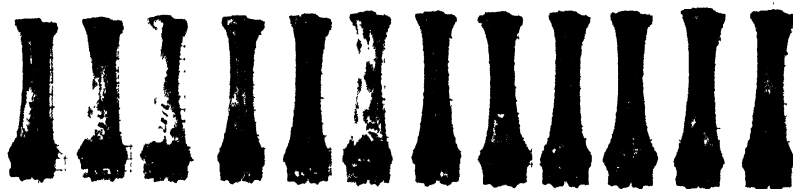
BURDEN LEICESTER X BLACKFACED



LEICESTER X CHEVIOT



OXFORD X BURDEN LEICESTER X HELLFIRE



SUFFOLK X BURDEN LEICESTER X CHEVIOT



SUFFOLK

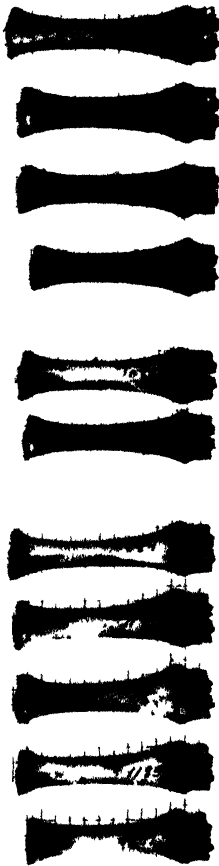


LEFT FORE CANNON BONE

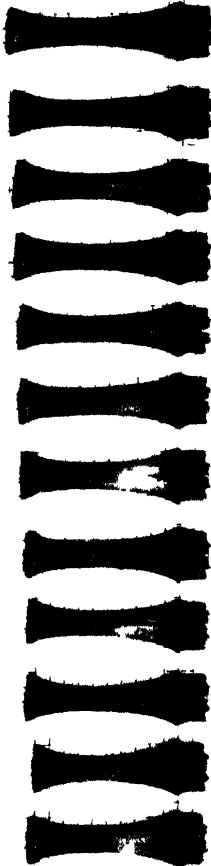
EFFECT OF BREED

HOGGETS ♂ WEIGHT CLASS 73-80 LBS

SUFFOLK X BORDER EXETER X CHEV. OT BORDER LEICESTER X CHEVIDOT OXFORD X BORDER LEICESTER X CHEV OT



5 6 7 8 9 10 11 12



LEFT FORE CANNON BONE

EFFECT OF WEIGHT

HOGGETS ♂

BORDER LEICESTER & BLACKFACED

WEIGHT CLASS 65-72 LBS



WEIGHT CLASS 57-64 LBS



WEIGHT CLASS 49-56 LBS



WEIGHT CLASS 41-48 LBS



WEIGHT CLASS 33-40 LBS



LEFT FORE CANNON BONE

EFFECT OF WEIGHT

HOGGETS ♂

SUFFOLK

WEIGHT CLASS 40-45



WEIGHT CLASS 40-45



WEIGHT CLASS 40-45



WEIGHT CLASS 45-50



WEIGHT CLASS 45-50



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